VOLUME XLII NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER, 1906

DIFFERENTIATION OF SEX IN THALLUS GAMETOPHYTE AND SPOROPHYTE.[1]

ALBERT FRANCIS BLAKESLEE.

(WITH PLATE VI AND THREE FIGURES)

IN a recent article (**5**) the writer has given a somewhat detailed account of zygospore germinations in certain species of the Mucorineae. The purpose of the present paper is to point out the bearing which the investigations already made in this group may have upon the questions of sexuality in other forms. Some of the problems for research which the facts observed in the mucors would suggest will be indicated, and it is hoped that in forms in which an alternation of generations occurs the distinction between differentiation of sex in the gametophyte and that in the sporophyte will be more clearly drawn than has been done previously. The various grades of differentiation in the gametes themselves or in the gametophyte and sporophyte will not be discussed. The subject for consideration rather will be the sexual condition in the plant as a whole.

According to the sexual character of their thalli, the species of the Mucorineae have been divided (**2–6**) into two main groups, homothallic and heterothallic—designations which correspond in the main to the terms hermaphroditic and dioecious respectively. In a homothallic species the thalli are all sexually equivalent, while in a heterothallic species the thalli are of two different kinds, which have been provisionally designated by the symbols (+) and (−). The sexual character of the (+) and (−) mycelia remains constant when

[1] This paper was written while working under a grant as research assistant of the Carnegie Institution, to whom the writer wishes to express his indebtedness for the opportunities for research afforded him.

they are grown separately in pure cultures. Thus the opposite strains of *Phycomyces* and *Mucor Mucedo* have been cultivated by means of sporangiospores to respectively 107 and 106 non-sexual generations without apparent change in their sexual behavior. This differentiation into (+) and (−) mycelia, which are capable of retaining their respective characters apparently for an indefinite number of vegetative generations, renders the heterothallic mucors as striking an example of dioecism as is to be found in the plant kingdom.

In those heterothallic species investigated in which a difference in vegetative growth is apparent, the (+) strain is the more luxuriant. In higher forms when a difference in size exists between the two sexes, the female is usually the larger. In such heterothallic forms the zygote develops entirely from the female thallus, and it would not seem unnatural that the thallus which supplies nourishment for the formation of the reproductive bodies should have a greater development than the thallus which produces only the comparatively small male gametes. The zygote of the heterothallic mucors, on the other hand, is formed by the union of morphologically equal gametes cut off from similar branches of the sexually opposite thalli. The zygospore is suspended midway between the (+) and (−) thalli which take equal share in supplying the nutriment for its development. The difference which sometimes exists in vegetative luxuriance between the two strains is independent therefore of the demands of the reproductive bodies, and is to be connected in some way with the primary sexual differentiation into the two opposite strains.

There are no heterothallic species as yet known in which a constant difference between the size of the two gametes has been observed. Two genera from the homothallic group are heterogamic, and in these forms the smaller gamete may be assumed to be male and the larger female. If it were found that a (+) test strain would show a reaction with the male, while the (−) strain showed a reaction with the female branch, one would have evidence for considering the (+) strain female and the (−) strain male. Unfortunately, attempts to hybridize test (+) and (−) heterothallic strains with these heterogamic forms have been as yet entirely unsuccessful. It is to be hoped that other heterogamic forms may be discovered which will lend themselves more readily to experiments in hybridization. That

as yet it has not been possible to substitute the terms male and female for (+) and (−), or *vice versa*, does not in the least detract from the conclusion, however, that the differentiation is a sexual one.

Forms characterized by gametes equal in size have been commonly classified as isogamous. The term, it need hardly be pointed out, can have only a morphological application among the mucors. Sexually the two gametes which unite have diametrically opposite characters. The mutual indifference of two mycelia of the same sex, and the active sexual reaction between mycelia of opposite sex which leads to the formation of zygospores when the mycelia are of the same species, and to the formation of imperfect hybrids when they are of two different species, indicate that the isogamy is by no means physiological. The classical researches of BERTHOLD (1) have shown that among the morphologically equivalent motile gametes of certain species of Ectocarpus there is a physiological differentiation into gametes which are attractive and those which are attracted, and a similar condition is met with among the Conjugatae. In the mucors the sexes seem to be equally attractive. If in other zygophytic forms the gametes are ever physiologically equivalent, their union can scarcely be considered a sexual process in the usual acceptation of the term.

The physiological differences which exist between the sexually opposite thalli of heterothallic mucors reaches morphological expression in those instances in which the (+) in comparison with the (−) strain is characterized by a greater vegetative luxuriance. Although the heterothallic forms are morphologically all isogamous, the sexual differentiation which they exhibit into two distinct races cannot be considered a lower grade of sexuality than the differentiation shown in the morphologically unequal gametes of the heterogamic species. Heterogamic forms are found only in the homothallic group. It would seem most reasonable to suppose that the isogamous homothallic forms were the more primitive, and had given rise on the one hand to heterogamic forms by a differentiation of the individual gametes, and on the other hand to heterothallic forms by a differentiation of the individual thalli. The partial transformation of the heterothallic species Phycomyces into a homothallic form which has been accomplished might, however, suggest the possibility of a deri-

vation of the homothallic forms from the heterothallic group. There are seven species known to be homothallic, among which three are heterogamic, while sixteen are known to be heterothallic. In all probability the large majority of the species which produce zygospores are heterothallic, yet the sexual character in but a small proportion of the mucors has been definitely determined, and it is unknown whether in this group species may not exist in which sexuality is entirely lacking. The writer has as yet no theories to offer as to the origin of sexuality in the group.

The fact that zygospores when germinating in a proper nutrient medium may give rise directly to a mycelium has led botanists to discard the idea of an alternation of generations comparable to that in higher plants, which was formerly seen in the succession from mycelia bearing sexually formed zygospores to germ tubes producing non-sexual sporangiospores which complete the cycle by the formation again of sexual mycelia. The cytological history of the formation and germination of the zygospores is at present too little known, and the writer would not care to be responsible for advocating as yet a too close homology between the conditions seen in the mucors and in the mosses for example, although the branching out of the germ tube under special conditions to form a mycelium might be considered of no great significance, since paralleled by the capacity of the moss sporophyte to give rise directly to a protonema. The gross analogy, however, between the germination of the zygote in mucors and that in the mosses is much more obvious than between the conditions in the mosses and those in the flowering plants or in animals (**9**), and is sufficiently close to justify one in concluding the mucors in a general comparison of the varying grades of sexual differentiation in the plant kingdom. In the accompanying diagrams and in the ensuing discussion, therefore, the same terminology will be applied to the mycelium and to the germ tube that has been found advisable for the gametophyte and sporophyte of forms in which it is at present orthodox to speak of an alternation of generations.

The terms dioecious, monoecious, and hermaphroditic have been used to designate varying grades of sexual differentiation, and have been applied to both gametophyte and sporophyte. Dioecism among

the bryophytes has been understood to signify the existence of two kinds of gametophytes, male and female, and the condition in the sporophyte has been disregarded; while among the flowering plants the usage is changed and dioecism has had reference solely to the sporophyte. An inspection of the accompanying diagrams will show that a plant which is monoecious as regards its sporophyte may be either monoecious or dioecious as regards its gametophyte; and on the other hand a plant dioecious in its gametophyte stage may be either monoecious or dioecious in its sporophyte stage. The first case is illustrated by the ferns, which are all dioecious in the sporophyte though having both conditions in the gametophyte; and the second case is illustrated by the flowering plants, whose sporophytes are either monoecious or dioecious, but whose gametophytes are always dioecious. In flowering plants and in ferns, one of the two generations is characterized by only a single sexual condition, and attention has accordingly been directed to the other generation in which both sexual conditions are present. That this inaccuracy in the terminology has been allowed to stand so long unchallenged is probably due to the tacit assumption that the condition in the ferns is typical for all the archegoniates. Up to the present time, however, the sexual condition in the sporophyte of forms below the ferns has never, so far as the writer is aware, been a subject of investigation or even of discussion.

The terms hermaphroditic, monoecious, and dioecious have established themselves in use, and have their place as technical designations in systematic botany of the flowering plants. As applied to the cryptogams, they have always been unsatisfactory, since the terms hermaphroditic and monoecious are used in descriptive botany to indicate whether the male and female sporophylls are produced in bisexual or unisexual flowers. In the cryptogams the terms lose their distinction with the passing out of use of the word flower. The greater or less local separation of the sexual organs or of the male and female sporophylls on a single individual is of little significance in comparison with the separation of the sexes on two entirely distinct individuals. Whether in Achlya, for example, the antheridia arise from the stalk which bears the oogonium as in *A. racemosa*, or are produced from separate special branches as in *A. prolifera*, is a

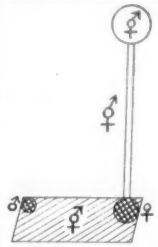
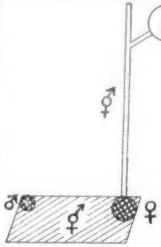
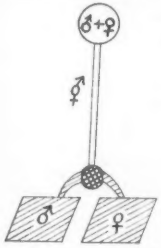
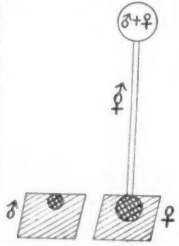
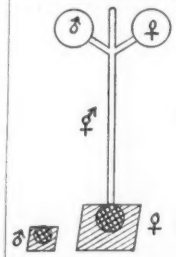
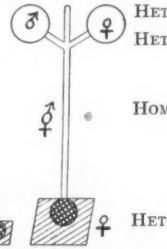
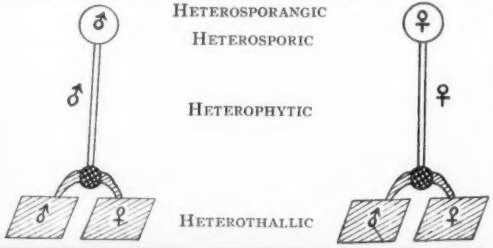
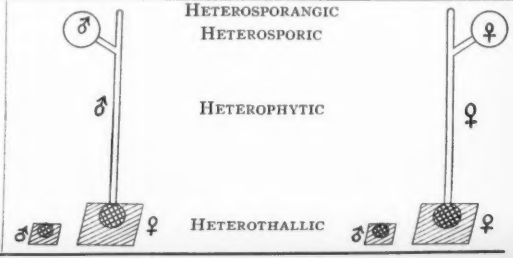
detail of somewhat minor importance. The sexual differentiation on a single mycelium in the latter species may be perhaps a forerunner of heterothallism, yet in each species the thallus as a whole is bisexual.

Rather than attempt to restrict the terms monoecious and dioecious to either the gametophytic or sporophytic stage, it has seemed best for the purposes of general discussion in the present article to avoid the ambiguity of the expressions now in use by applying a separate set of terms to designate the sexual condition in the gametophyte and sporophyte respectively. Whether or not the precision thereby gained will compensate for the disadvantages of adding new words to an already overburdened vocabulary of technical expressions must rest with botanists whose interest in the subjects of sexuality embraces all the groups of the plant kingdom.

Homothallic and heterothallic are terms already explained, which the writer has used to designate the species of the mucors characterized respectively by thalli sexually all alike, or by thalli sexually of two different kinds. Homothallic and heterothallic forms, therefore, have bisexual and unisexual thalli respectively, and the terms accordingly would correspond to the expressions monoecious and dioecious. Without changing the etymological significance, the meaning of the words homothallic and heterothallic may be appropriately extended to include a description of the degree of sexual differentiation in the prothallus or gametophyte of the archegoniates and spermatophytes, as well as in the thallus of the thallophytes.

Homophytic and *heterophytic* are offered as equivalents in the sporophyte of the terms monoecious and dioecious. Although the "plant" in the common acceptation of the word is the sporophyte in the higher forms, the condition is reversed in the bryophytes. The words homophytic and heterophytic, therefore, as designations for the sporophyte are etymologically not above reproach, but will suffice in lieu of a more cumbersome combination. The terminology suggested has reference to the sexual differentiation as such. The accompanying morphological differences are to be considered as secondary sexual characters and are not included in the classification.

It will now be possible to examine the sexual condition in the

MUCORINEAE	BRYOPHYTES	PTERIDOPHYTES	PHANEROGAMS
SPORODINIA	PHYSCOMITRIUM	POLYPODIUM	
HOMOSPORANGIC HOMOSPORIC HOMOPHYTIC HOMOTHALLIC	 HOMOSPORANGIC HOMOSPORIC HOMOPHYTIC HOMOTHALLIC	 HOMOSPORANGIC HOMOPHYTIC HOMOTHALLIC	
PHYCOMYCES	MARCHANTIA	SELAGINELLA	LILIUM
 HOMOSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HOMOSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HETEROSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HETEROSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC
MUCOR MUCEDO		POPULUS	
 HETEROSPORANGIC HETEROSPORIC HETEROPHYTIC HETEROTHALLIC		 HETEROSPORANGIC HETEROSPORIC HETEROPHYTIC HETEROTHALLIC	

BLAKESLEE on SEXUAL CONDITIONS

groups represented in the accompanying diagrams. In all the figures the gametophyte has been shaded with parallel lines, the antheridia and zygotes with cross-hatching; while the sporophyte and the sporangia have been left unshaded. The drawings are entirely diagrammatic, and no attempt has been made, therefore, to preserve the relative proportions of the parts figured. As has been already explained, the Mucorineae have been included in this scheme for the purpose of comparison, and the germ tube has been thus homologized with the sporophyte. The mucors then as represented in the first column in the diagram are the only group outlined in which all the three main types of sexual differentiation are as yet known.

In *Sporodinia grandis*, which may be taken as representative of the homothallic group, the mycelium (gametophyte), the germ tube (sporophyte), and the germ sporangia are all alike bisexual. The two opposed gametes, and perhaps the branches from which they are cut off, may not unreasonably be considered unisexual and of opposite sex. It has not been found possible as yet, however, to confirm this assumption experimentally. In the terminology adopted the species is to be considered homothallic, homophytic, homosporic, and homosporangic. The same condition is found in the "monoecious" mosses represented by *Physcomitrium pyriforme*, and in the homosporous ferns represented by Polypodium. The sporangium of the latter is represented as a side branch, since in the ferns, as also in the flowering plants, the sporangia are not simple terminations of unbranched sporophytes of limited growth, as in the bryophytes, but are borne on the sporophylls of a sporophyte more or less highly developed.

If the sexual character of the thallus be preserved, the spores and the sporophyte producing them must be also bisexual. There can be only one type therefore of homothallic forms. Of heterothallic forms, on the contrary, two types are possible—namely, those with bisexual sporophytes, *i. e.*, homophytic, and those with unisexual sporophytes, *i. e.*, heterophytic. These two types are represented by *Phycomyces nitens* and *Mucor Mucedo* respectively.

In the heterothallic species Phycomyces it will be convenient for the purposes of the present paper to neglect those instances in which the germination follows the *Mucor Mucedo* type, as well as the

occasional formation of homothallic spores in the germ sporangia, and to consider as typical the condition shown in the diagram. For a more detailed account of the zygospore germination in Phycomyces, as well as for the characters of the homothallic form into which this heterothallic species has been transformed, one must refer to the paper on zygospore germinations already cited. In the type, perhaps somewhat arbitrarily selected for discussion, the germinations are mixed—both male and female spores being produced in a single germ sporangium. The mycelia in this species are unisexual, the zygospores and germ tubes are bisexual, and the spores in the germ sporangia are unisexual. If the germ tube be forced to form a mycelium without the intervention of sporangiospores, a bisexual, *i. e.*, homothallic, mycelium results, which may produce typical homothallic zygospores. Phycomyces as discussed, therefore, is heterothallic, homophytic, heterosporic, and homosporangic.

In the bryophytes, *Marchantia polymorpha* is the only form which has been investigated in regard to the sexual condition of its sporophyte (cf. p. 170). Its gametophyte shows a differentiation into male and female thalli, and the germination of the zygote produces a sporophyte which bears a sporangium containing both male and female spores. Marchantia, therefore, like Phycomyces is heterothallic, homophytic, heterosporic, and homosporangic.

Selaginella, as a representative of the heterosporous ferns, follows in the main the Phycomyces type. It differs from Phycomyces and Marchantia, however, in that it is heterosporangic—the male and female spores being separated in microsporangia and macrosporangia. The spores themselves, moreover, are morphologically of two kinds, the female or macrospores being conspicuously larger than the male or microspores. This morphological differentiation of the spores and sporangia is known only in the heterosporous ferns and in the flowering plants, and is accompanied by a reduction in the size of the gametophyte. Among the homosporous ferns, prothalli are often found with only archegonia or antheridia, and investigators have been able to suppress the formation of one or the other in certain species where archegonia and antheridia occur normally side by side on the same prothallus. The writer is aware, however, of no form

among the homosporous ferns which investigators have shown to be strictly heterothallic.

In the monoecious and hermaphroditic phanerogams, illustrated by Lilium, the condition is essentially the same as in Selaginella, with a differentiation into macrospores and microspores, and like the latter species the type may be described as heterothallic, homophytic, heterosporic, and heterosporangic.

The homophytic division of the heterothallic group illustrated by Phycomyces is the only one of the three types that has representatives in all the orders outlined.

Mucor Mucedo represents the heterophytic division of the heterothallic group. In contrast to Phycomyces, the zygospores of this heterothallic species furnish pure germinations, but the spores are unisexual; and while the germ tube and the sporangiospores produced from one zygospore are male, those produced from another may be female. There are, therefore, two different kinds of germ tubes, of sporangiospores, and of sporangia, as well as two different kinds of mycelia. These elements in this species show no more recognizable morphological differences than its mycelia, although the sexual differentiation seems to be as marked as in forms in which such a morphological differentiation exists throughout the whole plant. *Mucor Mucedo* is heterothallic, heterophytic, heterosporic, and heterosporangic.

Since Marchantia is the only heterothallic form among the bryophytes the sexual character of whose sporophyte has been investigated, it is as yet unknown whether any forms of the mosses and liverworts exist corresponding to the *Mucor Mucedo* type.

No heterophytic forms are known at present among the heterothallic pteridophytes, and it will be impossible to say whether they ever existed in geologic times. The non-appearance of one reproductive form on a given sporophyte cannot be taken at once as proof that the species is heterophytic. It not infrequently happens, for example, that one finds only microsporangia on a single individual of Selaginella. Such instances may be compared to the suppression of the organs of one sex on the prothalli of homothallic ferns, and may equally be explained by assuming that the conditions necessary for the formation of the two reproductive bodies do not always coincide.

The "dioecious" phanerogams, represented by the heterophytic form Populus, follow closely the *Mucor Mucedo* type. They differ from *Mucor Mucedo* in that the sexual differentiation has reached a morphological expression, and the sex of the thalli, spores, and sporangia is at once distinguishable. In general the male and female sporophytes are alike in appearance, but in the sporophytes of some forms the sexes are easily distinguished. Perhaps the best known example among the common trees is the Lombardy poplar (*Populus pyramidalis*), which in male specimens has been widely cultivated for the sake of its pyramidal form. The female trees have a spreading habit of growth and are seldom to be found in cultivation.

In the diagram three squares are left blank. In the flowering plants heterothallism has become fixed and no forms of the Sporodinia type exist. There is no reason apparent why heterophytic forms should not occur among the heterothallic pteridophytes. The fact remains that all the existing heterothallic species are homophytic. The blank squares in the phanerogams and pteridophytes must therefore remain unfilled. Little is known about the sexual differentiation in the bryophytes, and it must rest with future research, therefore, to determine whether or not they possess heterophytic representatives in the heterothallic group.

In light of the conditions found in the Mucorineae, the heterothallic bryophytes, as already pointed out by the writer (*l. c.*, p. 25), offer a most interesting field for investigation. Accordingly attention was directed to the heterothallic form *Marchantia polymorpha*, which, according to the unpublished observations of NOLL as reported by SCHULTZE (**17**), retains the unisexual character of the individual thalli when propagated vegetatively by gemmae.

During the last November, Marchantia was found in fruit and sowings were made from individual sporangia, and the young plants resulting from their germination were isolated and transplanted in such a manner that at fructification it would be possible to determine the sex of the individual spores from which they were derived. While the present paper was largely in manuscript, the writer learned of unpublished observations made by NOLL on this same species. Professor NOLL, to whom the writer is greatly indebted for the information communicated, has cultivated Marchantia by means of gemmae

for over thirty generations of both male and female strains, without having been able to change the sexual character of the thalli by subjecting them to varying conditions of growth. The form is therefore strictly heterothallic. Moreover, in a single instance a sporangium was made to discharge its spores on a pot of earth, and male and female fructifications were obtained from the mixed growth of thalli resulting from their germination. Marchantia is therefore homophytic, and it now becomes possible to fill out in the diagram one of the two squares which in the bryophytes had been left blank pending the fructification of the young thalli which the writer had obtained from isolated spore germinations.[2]

In Phycomyces, with which Marchantia is to be compared, there seems to be no definite relation between the number of male to female spores formed in a germ sporangium, and it may even happen that all the spores are of the same sex. Moreover, it is not infrequently the case that in a small per cent. of the spores in a germ sporangium the segregation into male and female has not been completed. These bisexual spores produce homothallic mycelia. Cultures from individual spores will be necessary to determine for Marchantia the proportion of male to female spores in a single sporangium, and to ascertain if, in addition to the normally unisexual spores, bisexual spores are ever formed, as is the case in Phycomyces.

The bisexual germ tube of Phycomyces may be cut and forced to branch out to a homothallic mycelium. The observations of NOLL and of the writer have shown Marchantia to be homophytic. Its sporophyte as a whole, therefore, must be bisexual, and every cell formed before the determination of the sex of the spores, if brought to develop into a new plant, should theoretically produce homothallic individuals. PRINGSHEIM (**16**), STAHL (**18**), and CORRENS (**10**), among others, have obtained protonemata from the sporophytes of mosses. No one, however, seems to have succeeded in obtaining regeneration from the sporophyte of liverworts. The writer has experimented with mature sporophytes of Fegatella and with sporophytes of Marchantia of various ages, but has been unable to secure any growth from them.

[2] While the present paper is in press, 12 thalli have so far produced fructifications out of a total of 113 which were obtained from as many spores from a single sporangium. Of these nine are male and three are female.

In the investigation of the typical germinations of Phycomyces, it has been shown that the determination of sex does not occur in the zygote, but that an interval in the form of a germ tube is interpolated between the zygote and the germ sporangium where the segregation of sex finally occurs. The essential difference between Phycomyces and Marchantia lies in the fact that in the former the interval is a single-celled multinucleate structure arising from a multinucleate zygospore, while in the latter the interval is made up of many uninucleate cells arising from a uninucleate oospore. In Marchantia the segregation of sex undoubtedly takes place at some point in the maturation of the sporangium. If the archesporium and the spore mother cells prove capable of germinating, and it be possible in the thalli which result to recognize the presence of both sexes when the plants are homothallic, one may be in a position to determine the exact point where the segregation of sex occurs and to discover what relation if any the segregation may have to the reduction division or to other nuclear phenomena.

The predominance of organs of a single sex on the prothallus of the ferns due to conditions of growth and the similar phenomenon in the sporophyte of Selaginella may lead to the non-appearance of the other sex. Such a suppression of sex, however, is not to be confused with sex determination. By cultivating fern prothalli under unfavorable conditions of nutriment, PRANTL (15) was able to confine the production of sexual organs to antheridia. The archegonia demand a prothallus furnished with meristematic tissue, and consequently on a poorly nourished prothallus which has developed no meristem only antheridia can be formed. If prothalli which are producing exclusively antheridia be removed from a culture medium containing no available nitrogen, to a medium in which available nitrogen is present in sufficient amount, meristematic tissue is developed upon which archegonia are formed. KLEBS (12), moreover, has shown that by reducing the amount of light to which they are exposed prothalli may be brought to a prolonged vegetative growth, and thus the formation of both antheridia and archegonia may be suppressed. Professor KLEBS has informed the writer that when the amount of light is increased to a certain extent, antheridia alone are produced from these sterile prothalli,

but that to obtain archegonia, they must be exposed to a still greater illumination. BUCHTIEN (**7**) has shown that in Equisetum external conditions have a similar influence upon the apparent sex of the prothalli.

As yet attempts to influence arbitrarily the sex in unisexual plants have entirely failed. Even though it remain impossible to change the sex in the thalli of Marchantia, it may be found that, by experimenting on the sporophyte where we must assume the sex is unsegregated, one may be in a position to bring about the exclusive production of either male or female spores in a given sporangium. Such a result if accomplished would be analogous to the suppression of one set of sexual organs on the prothalli of ferns.

The behavior of the gametophyte of homothallic ferns and that of the sporophyte of such heterophytic flowering plants as *Melandrium album* (**19**) shows that, abnormally in certain forms and normally in others, only one sex may make its appearance. The conclusion suggested by an assemblage of facts, especially from the animal kingdom, is generally accepted that in so-called unisexual forms one sex is dominant and finds expression in the formation of gametes or spores of the given sex, while the opposite sex exists in a latent condition. However probable such a conclusion may appear for the majority of forms investigated, it must be admitted as at least a possibility that in certain plants or in certain stages a single sex may exist in a pure condition. The fact that besides the occasional production of unisexual germ tubes the zygote of Phycomyces gives rise typically to germ tubes in which the differentiation of sex has not taken place is proof neither for nor against the purity of the male and female thalli, and suggests that the not infrequent occurrence among heterophytic flowering plants of individuals with male and female flowers is as much an indication that both pure and mixed conditions may exist in the sporophyte of these plants as a proof that in heterophytic plants the opposite sex always exists in a latent condition. The germinations of the zygotes of Phycomyces and Marchantia suggest the possibility that the sex may be pure in the gametophyte while mixed in the sporophyte. The observations on unisexual plants, however, have been as yet confined almost entirely to the sporophytic stage, and little is known as to how strict

the differentiation of sex actually is in plants in the gametophytic stage.

Unless the gametes contain both sexes, parthenogenesis in homothallic forms should give rise to unisexual individuals—the male gamete to male and the female gamete to female individuals. So far as the writer is aware, no investigations have been undertaken with a view to confirm this assumption experimentally. Attempts made by the writer to determine the sexual character in the gametes of homothallic mucors by means of their germination before or after their transformation to azygospores have not as yet been successful. In the higher plants, parthenogenesis in the sense of the development of an individual from a sperm or egg cell with the reduced number of chromosomes is, so far as the writer is aware, not definitely known to occur. The sex in the apogamous seeds of Taraxacum for example, however, must contain male characters if the plants produced from them develop stamens, as seems regularly to be the case.

What the essential difference between sex actually is, is as yet beyond conjecture, and the significance of sex in organic development is at present a subject of conflicting discussion. It is to be hoped that a further study, especially of lower forms, where the gametes are more closely connected with the vegetative portions and the zygotes formed by their union more accessible to manipulation, may lead to a better understanding of some of the fundamental problems of sexuality. The present brief article is no place for any detailed discussion of sexuality in the various groups of plants. For a short general presentation of the subject, the reader may refer to the recent work of KÜSTER (**13**) and to the literature therein cited. It seems not out of place, however, to say a few words in regard to the thallic differentiation in the lower cryptogams, where the subject has received little attention.

Unisexual and bisexual forms occur throughout the plant kingdom, and are often to be found in the same genera. This sexual differentiation seems to have no relation to the stage of phylogenetic development. Thus while in higher animals the unisexual condition predominates, in higher plants the monoecious, *i. e.* homophytic, condition is the more common. Again, the majority of the ferns

are homothallic, while the majority of the mucors investigated are heterothallic. Both conditions, therefore, may be expected *a priori* in any group under investigation, whatever may be its phylogenetic rank.

In groups in which sexuality is present, in both fungi and algae, there are many forms for which the sexual spores have been but rarely found or are entirely unknown. The absence of sexual reproduction may be due (1) to constitutional sterility, (2) to conditions of growth unfavorable to the production of sexual organs, or (3) to the fact that the form is heterothallic and thalli of both sexes have not been found together. In the last case the apparent sterility would not be due to a lack but rather to an excess of sexuality which separates the male and female individuals. Even in heterothallic species, neutral races have been found to exist, and the conditions within which sexual reproduction is possible are frequently very limited.

A morphological investigation may suffice to show that the male and female organs are borne on the same thallus, and the form in question can then be at once classified as homothallic. A heterothallic condition, on the other hand, can never be recognized by a morphological investigation alone. The appearance of but one set of sexual organs on an individual form studied under the microscope may be due either to dichogamy or to suppression of the other sex brought about by conditions of growth, as well as to a unisexual character of the thalli. Carefully conducted cultures are therefore essential to a determination of the sexual character of forms investigated. A few examples may be briefly given to illustrate the necessity of employing the cultural method in a study of even well-known forms. Many other examples equally as appropriate will suggest themselves to the reader.

In the mosses the leafy shoots arise from an inconspicuous protonema, and if certain shoots bear only antheridia and others only archegonia, a cursory investigation would lead one to consider the forms heterothallic, especially if the antheridial and archegonial "plants" differ in appearance. *Funaria hygrometrica*, for example, is classified as monoecious by LIMPRICHT (**14**) and CORRENS (**10**), yet CAMPBELL (**8**, p. 187) says "Funaria is strictly dioecious." The

term here is perhaps used in reference to the constant separation of the sexual organs on different shoots without regard to their ultimate connection on the protonema; yet the latter is as an essential part of the plant as the leafy axis, and if the species is in fact homothallic it is not to be called dioecious. Such forms as Funaria offer an interesting field for regeneration experiments to determine if protonemata developed from antheridial and archegonial shoots differ at all in sexual character.

Among the algae, Spirogyra, to mention a simple example, is a familiar genus in which homothallic species are known to occur, and in which heterothallism is strongly to be suspected for certain species from a mere morphological investigation. In *fig. 1*, which is taken from STRASBURGER'S textbook, is represented *Spirogyra longata*. It seems in this type to be a matter of indifference whether the two conjugating cells come from the same or from different threads. Obviously here the filaments are bisexual and the species is therefore homothallic. In Debarya, represented in *fig. 2*, the zygospores are formed, as in the heterothallic mucors, midway between the two thalli, between which no differences are apparent. In the most common form of conjugation, however, which is represented in *fig. 3*, one filament seems to be receptive, since it contains all the zygotes formed between two conjugating filaments and has therefore been considered female. Though rather improbable, it is yet imaginable that a filament which acts as female toward one thread might function as male toward another. Theoretically it would not be a difficult task to determine by cultivation the sexual character of any form found producing zygospores.

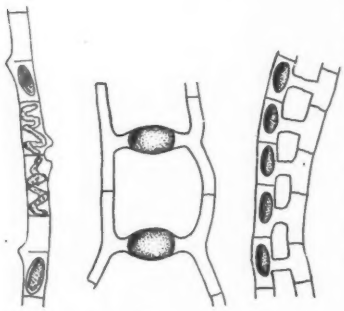


FIG. 1 Spirogyra FIG. 2 Debarya FIG. 3 Spirogyra

The Saprolegniaceae form sexually one of the most interesting groups among the fungi. In *Achlya racemosa* the antheridial branches are borne from the stalk of the oogonium, in *A. polyandra*

they arise fom differentiated branches which are only distantly connected with the hyphae which bear the oogonia, and in *Saprolegnia dioica* and *S. anisospora* we have forms which have been described as dioecious. Cultural investigation alone can determine whether these latter forms are in fact heterothallic. It is perhaps significant that in this group forms have been found which have remained sterile under cultivation (*cf.* HORN, **11.** p. 232). It is not improbable that they may represent unmated strains of heterothallic species.

Of especial interest will be an investigation for the possible occurrence of two sexual races in groups such as the desmids, the flagellates, and the infusoria, where the whole vegetative organism functions directly as the gamete.

Among the cryptogams, with the exception of the mucors and Marchantia, the sexual relations of the offspring from a single zygote in heterothallic forms, the zygotes of which give rise to more than a single individual, have never been investigated. The condition in the bryophytes has been already discussed under Marchantia. In the thallophytes writers see an alternation of generations variously expressed or suggested in the interpolation of carpospores between the fertilized zygote and the young plant. Whether in the heterothallic oedogoniums, to mention but a single example, the four carpozoospores formed at the germination of the oospore are always all of the same sex, like the germ spores in *Mucor Mucedo*, or may be some male and some female, like the germ spores in Phycomyces, can be decided only by an investigation of the individual thalli which they produce. If species in the Saprolegniaceae and Peronosporeaceae are found to be heterothallic, these forms will likewise furnish a fruitful field for investigation.

The discussion in the foregoing pages is based for the most part upon investigations done or already in progress in the Botanical Institute in Halle. The writer wishes to express his grateful appreciation to Professor KLEBS for the facilities of the laboratory and for his unfailing sympathy in the researches undertaken.

PARIS, April, 1906.

LITERATURE CITED

1. BERTHOLD, G., Die geschlechtl. Fortpflanzung der eigentlichen Phaeosporeen. Mitt. Zool. Stat. Neapel **2**:401–412. 1881.
2. BLAKESLEE, A. F., Zygospore formation a sexual process. Science N. S. **19**:864–866. 1904.
3. ——— Sexual reproduction in the Mucorineae. Proc. Am. Acad. **40**:205–319. *pls. 1–4.* 1904.
4. ——— Two conidia-bearing fungi, Cunninghamella and Thamnocephalis. Bot. Gazette **40**:161–170. *pl. 6.* 1905.
5. ——— Zygospore germinations in the Mucorineae. Annales Mycologici **4**:1–28. *pl. 1.* 1906.
6. ——— Zygospores and sexual strains in the common bread mould, *Rhizopus nigricans*. Science N. S. **24**: 118–122. 1906.
7. BUCHTIEN, O., Entwickelungsgeschichte des Prothallium von Equisetum. Bibliotheca Botanica **8**: 1887.
8. CAMPBELL, D. H., Mosses and ferns. 1895.
9. CHAMBERLAIN, C. J., Alternation of generations in animals from a botanical standpoint. Bot.Gazette **39**:137–144. 1905.
10. CORRENS, C., Untersuchungen über die Vermehrung der Laubmoose. pp. 472. *fig. 187.* Jena. 1899.
11. HORN, L., Experimentelle Entwickelungsänderungen bei *Achlya polyandra*. Annales Mycologici **2**:208–241. 1904.
12. KLEBS, G., Ueber den Einfluss des Lichtes auf die Fortpflanzung der Gewächse. Biol. Centralbl. **13**:641–656. 1893.
13. KÜSTER, E., Vermehrung und Sexualität bei den Pflanzen. Aus Natur Geisteswelt **112**:1–114. *fig. 38.* Leipzig, 1906.
14. LIMPRICHT, K. G., Die Laubmoose. Rabenhorst's Kryptogamen-Flora **4**:2.
15. PRANTL, K., Beobachtungen über die Ernährung der Farnprothallien und die Vertheilung der Sexualorgane. Bot.-Zeit. **14**:nos. 46 and 47. 1881.
16. PRINGSHEIM, N., Ueber Sprossung der Moosfrüchte. Jahrb. Wiss. Bot. **11**:1–6. 1878.
17. SCHULTZE, O., Zur Frage von den geschlechtsbildenden Ursachen. Archiv. Mikr. Anat. Entwickel. **63**:197–257. 1903.
18. STAHL, E., Ueber künstlich hervorgerufene Protonemabildung an dem Sporogonium der Laubmoose. Bot. Zeit. **34**: 689–695. 1876.
19. STRASBURGER, E., Versuche mit diöcischen Pflanzen. Biol. Centralbl. **20**: nos. 20–24. 1900.

A STUDY OF THE VEGETATION OF THE MESA REGION EAST OF PIKE'S PEAK: THE BOUTELOUA FORMATION.

II. DEVELOPMENT OF THE FORMATION.

H. L. SHANTZ.

(WITH SIX FIGURES)

IN an earlier paper[1] the writer has discussed the structure of the Bouteloua formation, and to this publication the reader is referred for general introductory matter. Space will not permit the inclusion here of lists of species in the formations of minor importance, which have to do with the development of this formation. The foothill thicket formation, the plains ruderal formation, and the plains bank formation are each made up of many species. Only the facies and a few of the more important principal species can be mentioned.

Invasion by formations.

FOOTHILL THICKET FORMATION.

This formation extends along the eastern base of the mountains and down along the ridges and gullies far out on the plains. It forms a distinct zone at the base of the mountains (*fig. 8*) and here occurs in its best developed form. In most places under natural conditions there seems to be an ecotone, a place of equal aggressiveness, between this formation and the Bouteloua formation.

FACIES: Cercocarpus parvifolius H. & A., Rhus trilobata Nutt., Quercus novo-mexicana (DC.) Rydb., Q. utahensis (DC.) Rydb., Q. Gambellii Nutt.

PRINCIPAL SPECIES: Rubus deliciosus James, Holodiscus dumosus (Nutt.) Heller, Ribes cereum Dougl., R. leptanthum Gray, R. pumilum Nutt.

In addition to those named there are about one hundred principal and secondary species.

This formation and the Bouteloua formation seldom mix, because where the shrubs grow the facies of the grass formation cannot exist. Nearer the mountains and along the hillsides they alternate sharply.

While the climatic and soil conditions are identical, the differ-

[1] BOT. GAZETTE 42:16–47. 1906.

ence in cover causes great difference in physical factors. Simultaneous physical factor readings show very clearly these differences. The following is a typical set:

Aug. 3, 1904, 10:45 a. m.

	Light	Temperature					Rel. humidity		Water content
		Soil	Soil surface	Plant surface	10^{cm}	1^{m}	10^{cm}	1^{m}	
Open.....	6s	24°	50°	44°	29°.6	28°.4	40%	32%	3.6%
Thicket (Quercus)	180s	18°	30°	28°.2	27°.2	26°.8	42%	39%	8.3%

FIG. 8.—Zonation at Palmer Park; frontal zone of *Bouteloua oligostachya* and *Artemisia frigida;* zone near base of the bluff *Andropogon furcatus;* at the base of the bluff the foothill thicket (Quercus); the bluff showing pine formation (*P. scopulorum*).

These conditions existed on the same exposures and 6^{m} apart. The open quadrat was dominated by *Bouteloua oligostachya* and *Artemisia frigida;* while the shaded quadrat contained *Quercus utahensis,*

Coleosanthus umbellatus, *Oryzopsis micrantha*, *Elymus condensatus*, *Filix fragilis*, and *Bryum argenteum*. The thicket was rather open, as may be seen at once by the light readings, the ratio of which is $\frac{1}{3}\frac{1}{0}$. This ratio often becomes $\frac{1}{6}\frac{1}{0}$, but is usually less for the greater part of the formation.

Along the ridges north and east of Colorado Springs there is certain evidence that the thicket formation is slowly pushing its way out into the grass formation. Of the shrubs *Cercocarpus parvifolius* seems best adapted for this invasion, and it is several miles in advance of any of the other dominant species (*fig. 9*). Nearer the mountains

FIG. 9.—*Cercocarpus parvifolius* invading the Bouteloua formation; pine formation on the horizon.

evidence is also found of the invasion of the grass formation by the thicket formation. This invasion, however, is not rapid. As soon as the young shrub is established or has grown to sufficient size to produce shade, the grass formation gives way rapidly to species

of the thicket formation. Among the first species to appear in the shade of these advancing shrubs are *Calochortus Gunnisonii*, *Mertensia linearis*, and *Stipa neo-mexicana*. Later, when the habitat has been rendered less xerophytic and when the other facies have entered, *Coleosanthus umbellatus*, *Oryzopsis micrantha*, *Elymus condensatus*, *Selaginella rupestris Fendleri*, *Filix fragilis*, and a number of other species appear.

Under perfectly natural conditions and without the intervention of herbivora, the thicket would undoubtedly replace the greater part of the grass near the mountains, but, as is seen later, the thicket is slowly giving way and the grass formation is advancing.

PLAINS RUDERAL FORMATION.

FACIES: Stipa Vaseyi Scribn., Puccinia Stipae Arth., Boebera papposa (Vent.) Rydb., Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Thelesperma intermedium Rydb., Verbena bracteosa Michx., Amaranthus blitoides S. Wats.

PRINCIPAL SPECIES: Salvia lanceolata Willd., Lappula occidentalis (Wats.) Greene, Polygonum aviculare L., Erysiphe Polygoni DC., Munroa squarrosa (Nutt.) Torr., Salsola Tragus L., Euphorbia glyptosperma Engelm., Malvastrum coccineum (Pursh) Gray, Puccinia Malvastri Pk., Vicia americana, Aecidium porosum Pk., Solanum rostratum Dunal, Helianthus annuus L., Cleome serrulata Pursh, Schedonnardus paniculatus (Nutt.) Trelease, Atriplex argentea Nutt., Senecio spartioides Torr. & Gray, Verbesina encelioides (Cav.) Gray, Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Picradeniopsis oppositifolia (Nutt.) Rydb.

The secondary species of this formation are very numerous.

The physical factors of this formation are practically the same as those given for the Bouteloua formation. The conditions of water content are such that the most common ruderals, eastern and European species, cannot thrive to the best advantage. Many native plants behave as ruderals and this name is applied to the formation. This formation represents many different stages in a succession which will result ultimately in the grass formation, and is always invaded by the plants of the grass formation. Only a few of the ruderal species succeed in the grass formation. The most important of these is *Boebera papposa*, occurring everywhere throughout the formation and sometimes very abundant. It is much better developed in a ruderal position and is regarded as a part of the ruderal formation. *Stipa Vaseyi*, another native plant, succeeds best in ruderal positions, but is often found as part of the formation.

The species of the ruderal formation are almost entirely native plants which readily invade any area from which the vegetative covering has been removed. Of the true ruderals, *Salsola Tragus* pushes its way into the formation proper. Here it occurs as dwarfed plants which seldom branch, and which die during the aestival period. *Leptilon canadense*, which occurs only here and there in the ruderal formation, also occurs throughout the grass formation. The plants are usually reduced to 10^{cm} in height.

PLAINS BANK FORMATION.

Whenever a ditch is made through the grass or other formations, or where the grass formation is irrigated, the bank formation comes in. It matters not what kind of soil, the presence of an abundance of water enables this formation to succeed. This, however, is not true invasion, and comes about only as a result of changed conditions which make the existence of the grass formation impossible. Good examples of the coming in of the bank formation may be found in irrigated meadows and in small areas where irrigation ditches or reservoirs have leaked.

A study of this formation is of the greatest interest, for it is along this formation that the eastern species find their way into the region. The reason is obvious, for here they find suitable conditions of water supply. As a result, it is here that the vegetation is made up of the most widely distributed species.

The mountain species find in this formation the cool temperature that enables them to exist away from their natural habitats. These species pass down along the brook banks, while the eastern species pass up along these same banks. The result is a varied flora.

The radical difference in water content between this formation and the Bouteloua formation does not permit of direct invasion. The following species, however, may occur in either formation: *Erigeron flagellaris*, *Agropyron occidentale*, *Helianthus annuus*, *H. petiolaris*.

The facies of the bank formation varies greatly with the age of the formation. In the ultimate stage they are as follows:

Populus deltoides Marsh., P. angustifolia James, P. acuminata Rydb., Salix spp., Prunus melanocarpa (A. Nels.) Rydb., P. americana Marsh., Rosa Sayi

Schwein., Ribes aureum Pursh, Clematis ligusticifolia Nutt., Symphoricarpos occidentalis Hook., Rhus trilobata Nutt.

In an earlier stage this formation is found best developed in the irrigated meadows where *Poa pratensis* L., *Eragrostis alba* L., *Juncus balticus* Willd., *Heleocharis palustris* (L.) R. & S., and *Medicago sativa* L. may rank as facies.

Fig. 10.—Floor of the pine formation (*P. scopulorum*) covered with the Bouteloua formation (*B. oligostachya*, *Koeleria cristata*, and *Artemisia canadensis*).

Xanthium commune and *Melilotus alba* are among the very first plants to enter on a newly formed ditch bank. In this formation are found many of the common species which occur in mesophytic situations in the eastern part of the United States.

PINE FORMATIONS.

As CLEMENTS[2] has pointed out, there are two pine formations near the base of the mountain range, the "foothill woodland" and

[2] Univ. Neb. Studies 4: no. 4. 1904.

the "pine." The first has as facies *Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.; and as principal species, *Stipa Scribneri* Vasey. The second has as facies *Pinus scopulorum* (Engelm.) Lem. and *P. flexilis* James.; and as principal species, *Arctostaphylos Uva-ursi* (L.) Spreng.

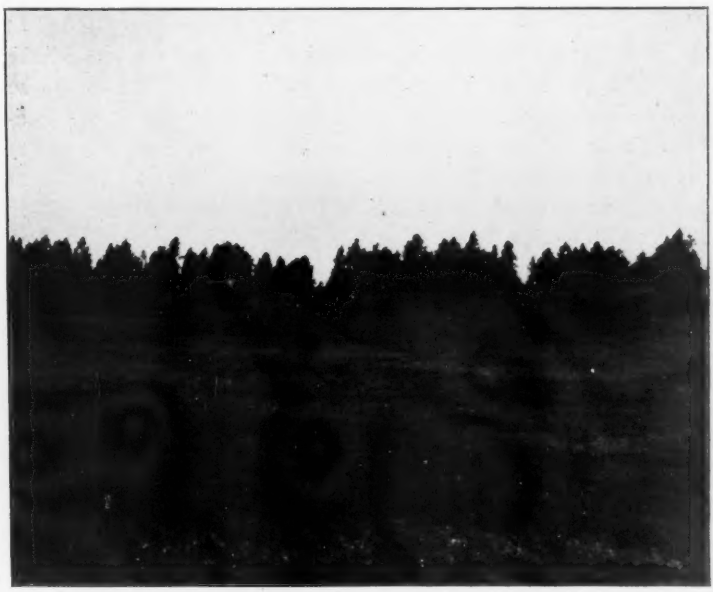


FIG. 11.—*Pinus scopulorum* invading the Bouteloua formation.

In the zone at the base of the mountains lies the foothill woodland formation, while just above is the pine formation. Each of these formations is invading the Bouteloua formation, and the one which lies higher on the mountains, the pine formation, is the more successful.

A consocies of this formation dominated by *Pinus scopulorum* has pushed its way eastward far into Nebraska[3] and carries with it many of the principal and secondary species. *P. flexilis* drops out before the foothills are reached. Near Eastonville, Colo., this formation

[3] POUND and CLEMENTS, Phytogeography of Nebraska, 2d ed., Lincoln, Neb., 1900, p. 336.

may be seen meeting the Bouteloua formation. All along this ridge the thicket formation has dropped out and the pines advance alone. The forest is not dense, and while many of the principal and secondary species are found on its floor, plants are also found which belong to the grass formation and which are able to survive in this location. In fact, the grass formation is found here in places dominating the floor of the pine formation—a true mixing of the formations (*fig. 10*). This mixing may be due to a certain extent to the entrance of the dominant species of the grass formation, but it is more likely to be the result of the gradual advance of the pines into the grass formation. This is shown very clearly in places where the young pines are several meters in advance of the older trees (*fig. 11*). This invasion may be observed along the ridge leading eastward from Palmer Lake and on which is found the so-called "black forest." Here the pines and the grasses mix and there are no shrubs present (*fig. 10*). The principal species, *Arctostaphylos Uva-ursi*, is also pushing out into the grass formation. A short distance west of Pring, Colo., this pine formation may be seen rapidly advancing along an old roadbed.

An entirely different condition may be observed eleven miles east of Colorado Springs. Here the pine formation is also advancing, but it is accompanied or rather preceded by the thicket formation. The advance of these two formations is favored by the cutting back of the gullies, forming steep hillsides, which offer the most favorable conditions for the growth of these two invading formations.

In many places the thicket, pine, and grass formations are found to meet and mix equally, the grasses forming the floor between the shrubs, and the pine scattered throughout. These three important formations are not only found meeting here on equal terms, but a remnant of an older formation, or at least one which gives evidence of greater age, is also found. This is the foothill woodland. *Juniperus monosperma* is scattered here and there and isolated trees of this species are often found which seem to be very old. Still stronger evidence is found in the fact that here, many miles removed from its fellows, is a very large and apparently very old *Pinus edulis*. Erosion has removed the soil from the base of the tree, exposing the roots, and it is certainly much older than any of the other trees

in this region. It is the only tree which supports a rich lichen flora.

Four important formations are found meeting and mixing here: the oldest, the foothill woodland, which has almost disappeared; the pine formation, which is slowly advancing; the thicket formation, which is also gradually advancing; and the grass formation, which gives way as the others advance. The thicket formation at this point entirely lacks the oaks, which fact is probably due to grazing.

In another part of the grass formation there is evidence of a slight advance of the foothill woodland. Young trees of *Juniperus monosperma* have established themselves in a few places on the mesa. In other places *Stipa Scribneri* is entering the plains region along with the thicket formation. The preponderance of evidence, however, seems to be in favor of a recession of this formation, and there is good reason to believe that it was at one time more extensive than at present.

Many species which seem to be most at home in the mountain formations also push down into the Bouteloua formation. Among these may be noted *Achillea lanosa*, extending down the draws, *Geranium caespitosum*, *Gilia pinnatifida*, *G. aggregata*, *Campanula petiolata*, and many other species.

Succession.

PRIMARY SUCCESSION.

On rock.

What the primary succession has been in this region cannot be determined. The succession on rock undoubtedly began with the lichen. On the most exposed rocks of the lime ridge *Staurothele umbrina* and *Lecanora previgna* are practically the only lichens found. On the other rocks the lichens are much more mixed and there seems to be good evidence of the accepted succession for lichens: first the crustose; then the more foliose forms like *Lecanora rubina* and *L. rubina opaca;* and finally *Parmelia conspersa*. On the mesa, where the rocks range from 5^{dm} in diameter to coarse gravel, *Parmelia conspersa* is the most important lichen, although *Rinodina oreina* and *Lecanora calcarea* are also common. *Placo-*

dium elegans, which is also common on rock, seems to require protection and is probably one of the later species to appear. The same may be said of *Lecanora subfusca allophana*, one of the important lichens, which succeeds best in crevices.

The rock lichens occurring within this region belong to the primitive lichen formation.

FACIES: Parmelia conspersa (Ehrh.) Ach., Rinodina oreina (Ach.) Mass.

PRINCIPAL SPECIES: Lecanora calcarea (L.)Sommerf., L. subfusca allophana Ach., L. previgna (Ach.) Nyl., L. rubina (Vill.) Ach., L. rubina opaca Ach., Placodium elegans (Link) DC., Buellia petraea montagnaei Tuck., Lecanora previgna revertens Tuck., L. xanthophana dealbata Tuck., Staurothele umbrina (Wahl.) Tuck.

SECONDARY SPECIES: Placodium cerinum (Hedw.) Naeg. & Hepp., Acerospora chlorophana (Wahl.) Ach., Biatora crenata dealbata Tuck., Heppia Despreauxii (Mont.) Tuck., Placodium vitellinum (Ehrb.) Naeg. & Hepp., Umbilicaria rugifera.

This formation occurs on all exposed rocks, with the possible exception of the Permian, which in most places disintegrates too rapidly to support a lichen flora. With the exception of the last four species, all of the species occur on exposed surfaces. The last four and *Placodium elegans* prefer shaded or at least somewhat protected situations. Throughout the mesa this formation has been almost completely replaced by the Bouteloua formation. On hills and more exposed rocky situations it is sometimes as important as the grass formation with which it alternates. With the more complete disintegration of the rocks this formation will entirely disappear.

On alluvium.

Uncertain as is our knowledge of the primary succession on rock, it is much more certain than our knowledge of the primary succession on alluvium. A careful study of the formation, and in particular those places which are least covered with vegetation, seems to aid in forming an idea of this primary succession.

Near Eastonville, in the region lying between the Bouteloua formation and the invading pine formation, an open area is being invaded by the following species: *Potentilla coloradensis*, *Thermopsis rhombifolia*, *Erigeron glandulosa*, *Paronychia Jamesii;* followed by *Arenaria Fendleri*, *Muhlenbergia gracilis*, *Bouteloua oliogostachya*,

Gutierrezia Sarothrae, *Artemisia canadensis*, and *Tetraneuris glabriuscula*. This is probably the best example of primary succession found by the writer. The absence of ruderal species is especially noticeable.

On the mesa the *Andropogon scoparius* consocies seems to be most primitive. In places not yet covered with vegetation, where the alluvium is nearest what it seems to have been originally, this grass is most abundant and together with *Eriocoma cuspidata* is the first to disappear in passing from this exceedingly open association to the more stable or closed Bouteloua formation. *Eriognum alatum*, *E. Jamesii*, *Tetraneuris glabriuscula*, and *Machaeranthera cichoracea* are generally present; but since they extend into the true Bouteloua formation they are probably not as much a part of the primitive association as the plants mentioned above.

The lime ridge vegetation is probably primitive, as shown by the following quadrat:

Lesquerella alpina	52	Oreocarya thyrsiflora	3
Gutierrezia Sarothrae	5	Gaura coccinea	1
Lithospermum linearis	4	Machaeranthera cichoracea	1

Total surface covered, 5 to 6 %.

At some distance from this, a quadrat shows the following:

Lesquerella alpina	31	Eriogonum Jamesii	3
Grindelia squarrosa	14	Boebera papposa	3
Hedeoma nana	13	Lithospermum linearis	1
Gaura coccinea	8	Salsola Tragus	2
Bouteloua oligostachya	6	Eurotia lanata	1
Aristida longiseta	4	Machaeranthera cichoracea	1
Stipa Vaseyi	3		

Total surface covered, 7 to 8%.

The entrance of Bouteloua is already noted, as is *Aristida longiseta*. A more distant point will show the following quadrat:

Bouteloua oligostachya	54	Lithospermum linearis	6
Atheropogon curtipendulus	28	Aristida longiseta	3
Grindelia squarrosa	16	Eriogonum Jamesii	2
Boebera papposa	57	Pentstemon angustifolius	1
Malvastrum coccineum	7	Salvia linearis	2
Lesquerella alpina	6	Stipa Vaseyi	1
Helianthus annuus	8	Salsola Tragus	2
Gutierrezia Sarothrae	13	Artemisia frigida	3
Chenopodium leptophyllum	10	Evolvulus pilosa	1

Total surface covered, 18 to 20%.

These quadrats are all on steep slopes where the soil is more or less broken. The first quadrat is in pure disintegrated limestone; some gravel has been washed into the second quadrat; while the third is a mixture of gravel, clay, and lime. The difference in soil is of no importance in this connection, since in other places the same succession occurs on the pure disintegrated limestone. In the first quadrat the water content varies from 19 to 6%; in quadrat 3 it varies from 19 to 2%; while in the second quadrat the per cent. of water is intermediate. As one passes from the first quadrat to the second and then to the third, the facies of the Bouteloua formation are found making their appearance; in fact, the flora, aside from a few ruderal species and *Lesquerella alpina*, is decidedly of the Bouteloua formation.

The native species, which are referred to as ruderal, show the greatest ability to occupy new ground and they are the most important in secondary succession. It seems reasonable to suppose that they were also very active in invading the newly formed alluvium, and that, if any of the existing species have taken part in the primary succession, these plants are to be sought among the native ruderals. This can be more clearly understood after a consideration of secondary succession.

SECONDARY SUCCESSION.

The repeated changes which have taken place in the formation of the great plains have manifestly been accompanied by changes in vegetation. What these changes have been can only be inferred from the changes which are now taking place wherever, in the process of erosion, there is a cutting away or deposition of material. These successions in a certain sense are primary, but will be discussed under secondary successions.

Biotic agencies.

There are so many chances for observing secondary successions that the experimental denuded quadrat was not deemed necessary, although several of these are now under observation. There are many trails which lead through the Bouteloua formation where the ground has been but slightly disturbed (*fig. 12*). The travel has simply worn off and killed the original vegetation. After having

been in use for a longer or shorter time they are generally abandoned. The soil is hard, in fact has never been broken, but since there is no vegetation, an opportunity is afforded for the entrance of new plants. These trails have not been used in wet weather, and they are therefore never cut up and no loose soil is formed. The succession here is first ruderals like *Boebera papposa*, *Amaranthus blitoides*, or *Verbena bracteosa*. These seem to be most successful

FIG. 12.—Trail invaded by *Boebera papposa;* Bouteloua formation at the sides.

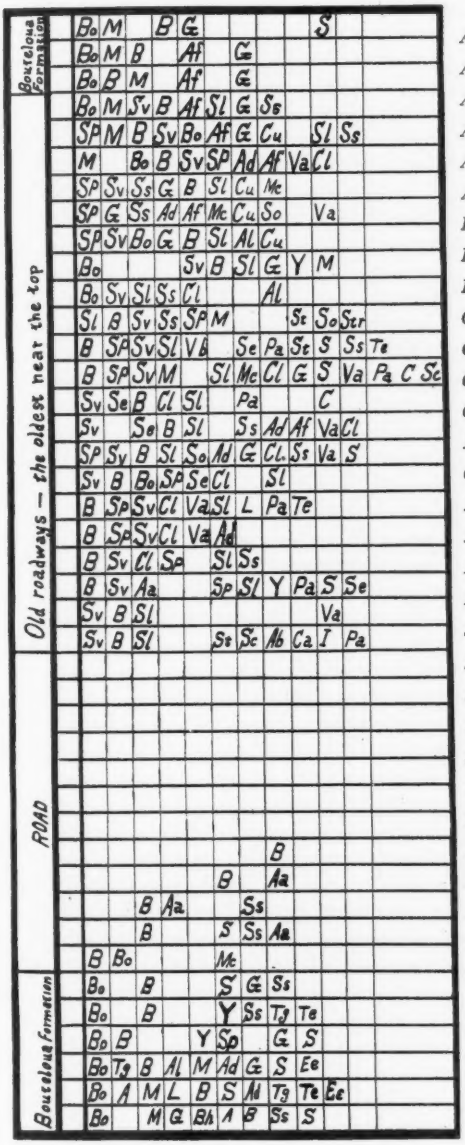
invaders of such trails. The grasses of the formation come in slowly, *Muhlenbergia gracillima* generally in advance of, or with *Schedonnardus paniculatus*, *Sitanion elymoides*, *Athero pogon curtipendulus*, and ultimately *Bouteloua oligostachya*. It is not an uncommon thing to find these old trails only distinguishable by the depression of surface and completely covered by the *Muhlenbergia gracillima* consocies. Where the same trail leads through the purer growth of *Bouteloua oligostachya*, it is not so rapidly covered, and when it passes through the *Bouteloua hirsuta* consocies it remains open for a still longer period.

The mesa road was originally of the type just mentioned. During wet weather the road would be cut up to a certain extent and drivers would then turn to one side in order to escape the rough road. The new path has always been formed on the southwest side. This road has been in constant use for several years with the result that plants have been destroyed continually on one side, and have invaded the old roadways from the other. These old roadways show a great many stages in succession.

The road is left in a somewhat roughened condition and the most important species to enter is *Stipa Vaseyi*. It thrives best in newer situations and disappears gradually as one passes back from the well-formed frontal zone. The stable condition which it brings about is not favorable for the growth of the seedlings and it dies out after ten to fifteen years. Aside from the entrance of the annual ruderals *Boebera papposa*, *Amaranthus blitoides*, and *Verbena bracteosa*, it represents the first stage in the succession which will result ultimately in the *Bouteloua oligostachya* formation.

The species which ultimately take possession are usually determined by the adjacent formation. Where *Muhlenbergia gracillima* is dominant it usually appears much in advance of *Bouteloua oligostachya*; but where the latter is dominant, it is usually in advance. *Stipa Vaseyi*, the first perennial to appear, is usually accompanied by the annuals *Boebera papposa*, *Salvia lanceolata*, *Polygonum aviculare*, *Amaranthus blitoides*, and a number of other species. The grasses enter in about the following order: *Schedonnardus paniculatus* followed by *Sitanion elymoides* and *Aristida longiseta*, and ultimately by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. With these grasses there appear many annual ruderals and also the following: *Senecio spartioides*, *Gutierrezia Sarothrae*, *Artemisia frigida*, *Carduus undulatus*, *C. plattensis*, and *Pentstemon angustifolius*.

A transect of the mesa road will give more detailed information regarding the sucessions found here (see transect). This transect is one meter wide. In the plot each division represents one meter, and the most important species in each square meter is placed at the left, and the other species in order of their importance are added to the right.



A, Atheropogon curtipendulus
Aa, Atriplex argentea
Ab, Amaranthus blitoides
Ad, Astragalus Drummondii
Af, Artemisia frigida
Al, Aristida longiseta
B, Boebera papposa
Bh, Bouteloua hirsuta
Bo, Bouteloua oligostachya
C, Calamovilfa longifolia
Ca, Cycloloma atriplicifolium
Cl, Chenopodium lepidophyllum
Cu, Carduus undulatus
Ee, Eriogonum effusum
G, Gutierrezia Sarothrae
I, Iva xanthifolia
L, Lappula occidentalis
Mc, Malvastrum coccineum
Pa, Polygonum aviculare
S, Sideranthus spinulosus
Sc, Sporobolus cryptandrus
Se, Sitanion elymoides
Sl, Salvia linearis
So, Senecio oblanceolatus
Sp, Schedonnardus paniculatus
Ss, Senecio spartioides
St, Salsola Tragus
Str, Solanum triflorum
Sv, Stipa Vaseyi
Te, Townsendia exscapa
Tg, Tetraneuris glabriuscula
Va, Vicia americana
Vb, Verbena bracteosa
Y, Yucca glauca

TRANSECT OF MESA ROAD.

This transect is typical of the greater part of the road. Near Gleneyrie *Machaeranthera cichoracea* appears in abundance in the frontal zone. At the lower end of the mesa road is found considerable variation. *Cleome serrulata* forms the frontal zone, and with this *Boebera papposa*, *Xanthium commune*, *Polygonum aviculare*, *Verbena bracteosa*, *Munroa squarrosa*, *Amaranthus blitoides*, *Solanum rostratum*, *Chenopodium album*, and *Malvastrum coccineum*. Just back of this, on a portion of the old roadway, is *Stipa Vaseyi*, with *Boebera papposa*, *Euphorbia dentata*, *Chenopodium leptophyllum*, *Ambrosia artemisiifolia*, *Sophora sericea*, *Polygonum aviculare*, *Schedonnardus paniculatus*, *Bouteloua oligostachya*, *Muhlenbergia gracillima*, *Artemisia frigida*, *Xanthium commune*, *Carduus undulatus*, *Iva xanthiifolia*, *Asclepias pumila*, and *Salvia lanceolata*. The advance on the graded graveled part is made almost entirely by annuals, *Boebera papposa*, *Verbena bracteosa*, *Amaranthus blitoides*, or in rare cases *Solanum rostratum* is most important, while other species are generally present in reduced numbers. The soil in these cases has been packed down and *Stipa Vaseyi* does not enter.

The old mesa road is not followed by the new in all places. In the lower end of the mesa it turns to one side. Here through the original formation, it was only a path. It had been worn down and when abandoned the soil, through the agency of frost and rain, had loosened and fallen in at the sides. This road is now revegetated with *Stipa Vaseyi*, which is in many places replaced by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. In one place this vegetation is practically identical with the formation.

The successions on trails vary considerably in different parts of the region. As one travels from Colorado Springs to Palmer Lake changes are soon noted. A short distance above Colorado Springs *Boebera papposa* becomes less abundant and the first species to invade the roadway is *Plantago Purshii*. Above Monument *Stipa Vaseyi* drops out as an invader, and the principal species which enter are *Polygonum aviculare*, *Lappula occidentalis*, *Verbena bracteosa*, *Amaranthus blitoides*, *A. retroflexus*, *Salvia lanceolata*, and *Rumex acetosella*. Below Monument a short distance the following succession was noted: The advancing zone was made up of *Lepidium*

apetalum, *Polygonum aviculare*, *Artemisia frigida*, *A. canadensis*, *Verbena bracteosa*, and *Plantago Purshii*; while farther back were found *Bouteloua oligostachya*, *Schedonnardus paniculatus*, *Chrysopsis villosa*, *Arenaria Fendleri*, *Gilia aggregata*, *G. pinnatifida*, *Senecio oblanceolatus*, *Gutierrezia Sarothrae*, *Koeleria cristata*, and *Sitanion elymoides*; followed by the Bouteloua formation in which *Bouteloua oligostachya*, *Stipa comata*, and *Arenaria Fendleri* were most important.

The stages of a succession which converts a denuded trail into the Bouteloua formation are not marked. First there is, as a rule, the entry of many annual ruderal species (*fig 12*). This in many cases is followed by *Stipa Vaseyi*, followed by *Schedonnardus paniculatus*, *Sitanion elymoides*, and *Aristida longiseta*, as well as many other secondary species of the formation, and these in turn by the facies of the grass formation. In some places *Stipa Vaseyi* does not enter and here may be found many other species. Among the more important are *Schedonnardus paniculatus*, *Gutierrezia Sarothrae*, *Chrysopsis villosa*, *Artemisia frigida*, *A. canadensis*, and many other species, followed by the facies of the grass formation.

Near Cheyenne Mountain a number of abandoned corrals show the following as the most important invading species: *Schedonnardus paniculatus*, *Artemisia canadensis*, *Solidago* sp., *Artemisia frigida*, *A. gnaphalodes*, and a number of secondary species—*Petalostemon purpureus*, *Thelesperma gracile*, *Chrysopsis villosa*, *Pulsatilla hirsutissima*, *Lacinaria punctata*, *Sporobolus cryptandrus*, *Aristida longiseta*, *Bouteloua hirsuta*, *Aragallus Lambertii*, and the ruderals *Boebera papposa* and *Euphorbia glyptosperma*.

A denuded quadrat showed during the third summer *Artemisia canadensis*, *Geranium caespitosum*, *Pulsatilla hirsutissima*, *Chrysopsis villosa*, and *Artemisia ludoviciana*. A second corral showed *Artemisia canadensis* and *A. frigida* as the chief invaders, with many other species coming in, of which those most important are *Schedonnardus paniculatus*, *Bouteloua oligostachya*, and *Koeleria cristata*.

The early stages of these successions vary greatly. In the study of a large number the following plants are found to enter first: *Boebera papposa*, in the mesa region and adjacent areas; northward toward Palmer Lake, *Plantago Purshii* or *Polygonum aviculare*;

and farther east *Picradeniospsis oppositifolia*, sometimes accompanied by *Malvastrum coccineum*.

A number of graded roads have been built very recently and these show only the very first vegetation, a ruderal annual vegetation. The boulevard, which runs from Colorado Springs to Manitou, is an older road of this type, having been built for about thirteen or fourteen years. The first permanent succession on this road within the Bouteloua formation was *Stipa Vaseyi*, which is now giving way to *Muhlenbergia gracillima* and *Bouteloua oligostachya*. Many other species came in, among which the more important are *Sitanion elymoides*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Helianthus annuus*, *Quincula lobata*, *Astragalus bisulcatus*, *Sophora sericea*, *Grindelia squarrosa*, with other plants from the formation, as well as ruderal species.

One of the transects of this road deserves special mention. There is a cut here of about 2^m, and the road runs north and south. The differences in the east and west sides are due entirely to the differences in exposure, and to its effect upon temperature and water content. The west side, which receives the most light, has first a distinct zone of *Petalostemon oligophyllus*, back of which there is a mixed zone of *Boebera papposa* and *Xanthium commune;* this is followed on the bank by *Stipa Vaseyi*, and this in turn by a crest zone largely of annuals. The east side shows first a zone of *Xanthium commune* followed by *Stipa Vaseyi*, mixed with *Schedonnardus paniculatus*, *Boebera papposa*, *Psoralea tenuiflora*, etc.; and this is followed on the steep unstable soil by annuals. Back of the annuals is the Bouteloua formation in which *Muhlenbergia gracillima* predominates.

There is a great deal of variation in the species which first appear. Almost any one of the species cited under the ruderal formation may dominate in certain places, but the more or less typical examples mentioned above should serve to give an idea of the succession on roads.

Reservoirs are generally built where only one side needs to be dammed. The outer slope of the dam is invaded in the same way a road would be. An interesting exception is found at Palmer's reservoirs. The large reservoir, which was built in 1902, had by

1904 covered the bank chiefly with *Stanleya glauca* and *Mentzelia decapetala*. A great deal of the soil of this bank was hauled in from the lime ridge region, and with it, the seeds of *Stanleya glauca* were carried in. In one of the other reservoirs, which is several years older, *Medicago sativa* was predominant. Normally, *Boebera papposa*, *Stipa Vaseyi*, and other ruderals would be expected to appear first.

A new reservoir constructed on the mesa in 1904 showed during 1905 the following species: *Boebera papposa*, *Salsola Tragus*, *Senecio spartioides*, *Artemisia frigida*, *Senecio oblanceolatus*, *Argemone intermedia*, *Mentzelia nuda*, *Polygonum aviculare*, *P. Douglasii*, *Euphorbia robusta*, *Yucca glauca*, *Chenopodium album*, *Gaura coccinea*, *Cleome serrulata*, *Petalostemon purpureus*, *Amaranthus blitiodes*, and *A. retroflexus*.

In building roads and reservoirs it often happens that several meters of surface soil and all the vegetation is removed. Succession is different here from the places already mentioned. The annual ruderals do not appear in such great numbers. Among the species which enter are *Argemone intermedia*, *Mentzelia ornata*, *Petalostemon oligophyllus*, *P. purpureus*, *Sitanion elymoides*, *Aristida longiseta*, *Munroa squarrosa*, and other common hillside plants, since the soil here is usually gravel.

Broken areas.

Here and there on the plains are found areas which have been plowed and planted, but have been abandoned because of the scanty water supply. The succession of plants here is much the same as on graded roads, but is usually more uniform. An abandoned garden patch showed the following year the facies *Anogra albicaulis*, with *Chenopodium album* and *Helianthus annuus* as the principal species. An area on top of the mesa showed almost a pure stand of *Boebera papposa;* while still another showed *Schedonnardus paniculatus*. *Artemisia frigida* sometimes enters denuded areas and dominates the early stages of the succession. During 1904 a tract was seeded with *Lolium perenne;* the following summer it showed *Boebera papposa* and *Verbena bracteosa*, as well as *Polygonum aviculare*, *Salsola Tragus*, *Artemisia frigida*, *Lolium perenne*,

Solanum triflorum, *Senecio oblanceolatus*, and *S. spartioides;* also a very few young plants of *Yucca glauca*, *Argemone intermedia*, *Carduus undulatus*, and *Tetraneuris glabriuscula*.

The usual flora on the hills of the prairie dog is *Anogra coronopifolia*, *Malvastrum coccineum*, *Munroa squarrosa*, *Amaranthus blitoides*, *Picradeniopsis oppositifolia*, *Boebera papposa*, and *Artemisia frigida*. *Muhlenbergia gracillima* is the most effective in reclaiming the old deserted hills. In fact, in looking over a deserted dog town the location of the old dog hills can be determined at once from the fact that although the surrounding vegetation is dominated by *Bouteloua oligostachya*, the location of the old hills is marked by a community of *Muhlenbergia gracillima*.

Near Pring, Colo., an abandoned field showed the first year *Helianthus petiolaris*, with a less amount of *Boebera papposa*, *Malvastrum coccineum*, *Solanum rostratum*, *Lappula occidentalis*, *Verbena bracteosa*, and a very few plants of *Artemisa frigida*, *Atheropogon curtipendulus*, *Schedonnardus paniculatus*, *Carduus undulatus*, and *Eriogonum annuum*. Here are found three very distinct sets in the succession. First, annual species, followed by a group of ruderal species, and this in turn by perennials from the Bouteloua formation. In another place *Thelesperma intermedium* was the first species to enter. Near Falcon, Col., an abandoned field showed after two years *Helianthus petiolaris* and also *Munroa squarrosa*, *Lappula occidentalis*, *Chaetochloa viridis*, *Plantago Purshii*, *Amaranthus retroflexus*, and *Ptiloria ramosa*. In some places *Bouteloua oligostachya* was entering. Another field which had been abandoned for about eight years showed *Sporobolus cryptandrus*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Cenchrus tribuloides*, as well as *Senecio oblanceolatus* and *Munroa squarrosa*, a few annuals, the more important of which were *Helianthus petiolaris*, *Verbena bracteosa*, and *Cryptanthe ramosissima*. Into this area *Bouteloua oligostachya* was pushing its way and had in places near the edge of the field almost replaced the other species.

Several miles west and south of Fountain, Col., a most interesting stage of succession is shown. The surrounding vegetation is of the *Bouteloua oligostachya* consocies with very few primary and secondary species. An area which had been broken and abandoned showed

the *Muhlenbergia gracillima* consocies almost entirely replacing the earlier stages of the succession. A very little *Boebera papposa* and *Schedonnardus paniculatus* remained, while about an equal amount of *Bouteloua oligostachya* was invading and will after a number of years replace the Muhlenbergia.

As long as the ants are alive, they remove all vegetation for some distance around their hills. In low places *Cleome serrulata* may form a semicircular zone on the lower side of this denunded area. *Helianthus annuus*, *H. petiolaris*, *Stipa Vaseyi*, and many other species may also be found in this situation. The most common plant to develop in this area is *Munroa squarrosa*, which often forms a perfect zone.

Erosion.

The dry soil is easily washed away by heavy rains. This forms loose soil at the base of the hills and also leaves broken places from which the soil is removed. On the hillsides there are often produced natural terraces, each of which ends in a broken edge. During the rains these terraces are cut back and new soil is exposed. These places may be occupied by *Boebera papposa*, *Salsola Tragus*, or other annuals, but generally *Stipa Vaseyi* is the invading species. Here it serves to bind the soil and prepare the way for *Muhlenbergia gracillima* and *Bouteloua oligostachya*.

In the low draws there is generally a hollow washed out below the terrace, and as a result of the falling in of the soil when dry there is found both loose and undisturbed soil. These places are marked by a growth of *Stipa Vaseyi*, with *Boebera papposa*, *Solanum rostratum*, and often *Salvia lanceolata*, *Helianthus annuus*, *Verbena bracteosa*, *Salsola Tragus*, *Xanthium commune*, and *Leptilon canadense*. Places such as this are very much like the ordinary draw where more or less of the soil which was washed down from the hills is deposited. Conditions here are also almost the same as in the alluvial fans which are formed at the bases of all the ravines, whether they be small or large. Here new soil is deposited during every heavy rain, and as a result the slow growing grasses such as *Bouteloua oligostachya* and *Muhlenbergia gracillima* cannot thrive. *Stipa Vaseyi* is the most successful plant of such habitats. It marks the

dry water courses and also all of the alluvial fans. Succession here is practically the same as on any ruderal area. In addition to *Stipa Vaseyi* there is usually found *Boebera papposa*, *Salvia lanceolata*, and in some cases *Xanthium commune* and *Cleome serrulata*. When the soil has become more stable *Stipa Vaseyi* slowly gives way. *Artemisia frigida* is now one of the first species to appear, and is often dominant after *Stipa Vaseyi* has disappeared entirely. This

FIG. 13.—Blow-out; the prominent plants are *Muhlenbergia gracilis*, *Meriolix serrulata*, *Artemisia canadensis*, and *Andropogon scoparius; Calamovilfa longifolia* in the background.

is followed by *Muhlenbergia gracillima*, and after a number of years this is replaced in turn by *Bouteloua oligostachya*.

On dry sandy ridges blow-outs are often found (*fig. 13*). The succession here is usually *Polygonella articulata*, *Cycloloma atriplicifolium*, *Carex* sp., *Muhlenbergia gracilis*, *Sporobolus cryptandrus*, *Artemisia canadensis*, *Thelesperma gracile*, *Eriogonum annuum*, *Meriolix serrulata*, *Chrysopsis villosa*, and *Andropogon scoparius*.

The most important plant occupying the alluvium deposited by permanent streams is *Melilotus alba*. Species of minor importance are *Juncus bufonius* and *Riccia crystallina*.

ANOMALOUS SUCCESSION.

When biotic or physical agencies bring about sufficient change in the habitat, the result is an anomalous succession. The change of habitat may be gradual and yet the effect on the succession be such as will change entirely the ultimate formation. We may also have the succession interfered with in such a way as to hasten the ultimate formation, to cause it to become more stable in a shorter time, or to retard the succession or reduce it to a more primitive condition.

Due to grazing.

The influence of grazing is very clearly seen by comparing fenced areas with those that have not been protected from grazing animals. Cattle, and to a less extent horses, are the only animals that have grazed within this region in recent years.

Near the lower end of the mesa is Colorado City, the old territorial capital of Colorado and known as one of the oldest towns in the state. For fifty years it has been the custom to have a herd boy drive the cattle out on the adjacent areas to graze each day and bring them back each night. Colorado Springs, a more recent city, also sends its herds out on the same area. It will be well, at first, to see what effect this has had upon the Bouteloua formation. In those parts of the formation where grazing has not played a part the formation is very open, while in the grazed portions it is more closed. In the open formations many species appear with the grasses, while in the more closed formation these species are almost entirely absent. A typical quadrat from the south mesa which has been grazed shows the following species:

Muhlenbergia gracillima	23	33%	Sideranthus spinulosus	3
Bouteloua oligostachya	24	12	Malvastrum coccineum	5
Atheropogon curtipendulus	1		Townsendia exscapa	2
Artemisia frigida	2		Echinocereus viridiflorus	1
Boebera papposa	36			

Total surface covered, 45 to 50%.

In some of the draws the preponderance of *Muhlenbergia gracillima* is even more marked. Near the above quadrat, in a portion protected from grazing, a quadrat would show:

Bouteloua oligostachya	18 %	Artemisia frigida	1
Muhlenbergia gracillima	2.5	Artemisia gnaphalodes	1
Aristida longiseta	2.5	Gutierrezia Sarothrae	2
Chrysopsis villosa	8	Sitanion elymoides	1
Thelesperma gracile	9	Eriogonum alatum	2
Echinocereus viridiflorus	4	Pentstemon angustifolius	1
Opuntia polyacantha	3	Carex pennsylvanica	5
Euphorbia robusta	1		

Total surface covered, 27%.

In a portion of the mesa which has been grazed, but not to such an extent as the first quadrat given, is found:

Bouteloua oligostachya	22%	Artemisia frigida	5%
Muhlenbergia gracillima	7		

It cannot be stated positively that this condition is entirely due to grazing. It seems likely, however, that grazing would favor the development of grasses and tend to destroy the other plants, particularly the dicotyledons. There is a very noticeable difference in adjacent areas when one is protected from grazing. The preponderance of *Bouteloua oligostachya* and *Muhlenbergia gracillima*, and the paucity of higher spermatophytes in the grazed area is the chief difference. This seems to be the exact condition which would come about by natural succession and the grazing in this case hastens this succession. The more primitive parts of the formation and those which have not been grazed are much alike. Grazing, when not too severe, favors the development of the facies of the formation.

Still another condition due to grazing should be considered. Near Colorado City, and particularly in the region lying between Colorado City and Colorado Springs, the grazing has been very severe. The result here has been first to drive out most plants other than the grasses, and ultimately even to destroy *Bouteloua oligostachya* and *Muhlenbergia gracillima* to a great extent. A few plants, such as *Astragalus bisulcatus*, *Chrysothamnus graveolens*, *Grindelia squarrosa*, and others which are not touched by grazing animals, still survive; but the character, aside from a few of these species, is now almost entirely marked by annuals. The succession has

become practically that which follows on a denuded area. *Salvia linearis*, *Atriplex argentea*, and *Bouteloua prostrata* are here the principal species. With these are found many of the ruderal plants as well as the following important perennials: *Agropyron occidentale*, *Astragalus bisulcatus*, *Sophora sericea*, *Vicia americana*, and a very little *Bouteloua oligostachya*, *Quincula lobata*, and *Phyllopterus montanus*.

The effect is to delay the succession or to cause it to return to a more primitive condition. The grazing does not change the Bouteloua formation into another formation, since grasses seem to be especially adapted to these conditions.

The effect of grazing is very different on the thicket formation. Wherever cattle are allowed to crop the thicket formation very closely, the facies are completely killed. This is the most noticeable in the case of the oaks, which are killed by the entire loss of chlorenchyma tissue. They are attacked by cattle before any of the other facies of the thicket formation.

An examination of the region shows that on the mesa near Colorado City the thicket formation has been replaced almost entirely by the Bouteloua formation. Only scattered bushes of *Cercocarpus parvifolius* and *Rhus trilobata* are found and these much reduced in size. The explanation lies in the fact that this portion has been grazed more than the part which is farther removed from Colorado City. The remnant of the old thicket can be seen in many places, and the stages in the succession which have produced a grass formation instead of a thicket formation may be traced. There is a scanty plant growth under these shrubs. When they are killed outright the space is open to plant invasion, and as a result the ruderals come in in abundance. *Chenopodium album* may be one of the forms which appears at this time, especially if the cattle have destroyed most of the under vegetation. At other places where the shrubs have been cut down the succession may be much the same as the ruderal succession and result in the typical Bouteloua formation. As a rule the shrubs are gradually reduced in size. The result here is that the grasses slowly encroach upon the area as the shrubs are eaten lower, and as the clump becomes more open the undergrowth increases. *Agropyron occidentale*, *Stipa comata*, *S. neo-mexicana*, *Atheropogon curtipendulus* come in slowly; *Coleo-*

santhus umbellatus and *Chenopodium Fremontii* disappear. When the shrub ultimately dies and breaks up, there is a very small ruderal place in which the succession is identical with that already described for denuded places. Grazing changes the thicket formation to a grass formation, and the more rapid the change the more nearly it approaches the ordinary ruderal successions.

Due to drainage.

Drainage is not an important factor, but it seems best to consider here those changes which result when an irrigated area is left without irrigation, a ditch abandoned, or the water of a stream turned aside causing the bed to become dry.

Examples of the first case mentioned are not found excepting where, because of lack of attention, the water does not flow evenly over a meadow. The succession here is gradual, forms like *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* taking the place of the more hydrophytic grasses and rushes. If the change of habitat is abrupt, most of the species die and a ruderal succession follows. When the change is very gradual, the species mentioned above, together with *Agropyron occidentale*, take the place of the rushes. *Bouteloua oligostachya* often appears in this stage of the succession, but *Muhlenbergia gracillima* is one of the last to appear.

In abandoned ditches a mixed formation is generally found. In this habitat the following species of the mesophytic bank formation may continue for a long time: *Clematis ligusticifolia*, *Xanthium commune*, *Symphoricarpos occidentale*, *Stachys palustris*, *Erigeron flagellaris*, and *Vicia americana*. The last two species are elements of the Bouteloua formation and are able to adapt themselves to the change of habitat. Of the grasses of the Bouteloua formation, *Bouteloua oligostachya* and *Agropyron occidentale* are the first to enter. They appear much earlier than *Muhlenbergia gracillima*, and thrive even better in these transformed ditches than in the Bouteloua formation proper.

There is only one example of the effect of a change in the natural water course. This is not complete, but enough water has been taken from Camp Creek to cause it to be dry for a greater part of the year. The first and most noticeable effect has been the death of

the trees, *Populus angustifolia* and *P. deltoides*. This condition has obtained for only about three years, and the effect thus far has been destructive. The bank species, with the exception of those that are able to exist in more xerophytic habitat, have died, and aside from the entrance of a very few ruderals there has been no marked succession as yet.

Due to irrigation.

The changes produced by irrigation are complete and varied. Where a ditch passes through the Bouteloua formation in places where there is seepage, the first stages of the succession which lead to the irrigated meadow formation are found. The effect here is usually the better development of *Agropyron occidentale*, and at the same time the disappearance of *Muhlenbergia gracillima*. *Bouteloua oligostachya* also grows more rank than where not irrigated. This succession is exceedingly variable, probably because of the variable water supply, and the stage of the succession is an index to the amount of water added. In some places the meadow flora is reduced largely to rushes and other hydrophytic plants, while in other places *Bouteloua oligostachya*, *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* are most important.

In the bank formation the conditions are varied. Between the water and the xerophytic formation through which the stream or ditch runs, there are all gradations from hydrophytic to xerophytic. But to divide this formation in regard to water content of the soil would not be practicable. Another condition makes the formation more complex. In the ditch formation, there is, besides the invasion of the mesophytic and hydrophytic plants, the entrance of the ruderal. When the ditch is first made the ruderal formation makes its appearance. At almost the same time the mesophytes and hydrophytes appear. The ruderal formation always tends towards self destruction. Here the result is that the outer portion of the ditch is ultimately occupied by the characteristic Bouteloua formation, while on the inner the more mesophytic bank species become established. In the ultimate bank formation the line of separation from the grass formation is very distinct.

Along many of the irrigation ditches a condition prevails which

prevents the development of the ultimate stage of the succession. Each year the bottom of the ditch fills up with silt which is removed to the bank the following spring. This forms a new soil for the entrance of ruderal species, and as a result the bank returns to a somewhat primitive condition.

Another factor of importance here is the fact that during the winter the ditch is empty the greater part of the time. This condition is detrimental to the success of the species of the ultimate formation. The result is that along these irrigation ditches are found various stages of anomalous successions, which are checked repeatedly, or even turned back by the reversion to more primitive conditions. The successions are interrupted again and again, and this may account to a great extent for the variable character of the bank formation.

General discussion.

After careful study it is at once apparent that all parts of the formation are not of the same age. The secondary successions throw much light upon the structure as well as upon the development of the formation. These exhibit rather well-marked stages. The first is a ruderal consocies; the second, a society of the formation; while the ultimate stage is a consocies of the formation. All of these successions lead undoubtedly to the Bouteloua formation.

The successive deposition and erosion which has produced the Great Plains does not differ markedly from that which may be noted at the present time. The vegetation on new deposits of soil passes through the typical succession leading from the ruderal to the grass formation. Near the mountains the cutting back of the gullies results in the establishment of the thicket formation, which is preceded usually by the entrance of many of the secondary species of the thicket and grass formation. The pine formation is usually mixed with the thicket formation. When this cutting back of the gullies exposes rocks of a sufficient degree of stability, the primitive lichen formation precedes all others.

In many places gullies are cut back which are reclaimed at once by the grass formation. The thicket and pine formations do not enter. In these places the *Andropogon scoparius* consocies usually becomes established.

The elevated dry ridges are occupied by the *Selaginella densa* formation in which *Paronychia Jamesii* is a prominent species. This evidently represents a younger stage in a succession which will give ultimately the Bouteloua formation. Among the most important invading species are *Stipa comata, Koeloeria cristata,* and *Bouteloua hirsuta.*

If these ridges are sandy, blow-outs often occur which result when reclaimed in the *Calamovilja longifolia* consocies (*fig. 13*). This consocies thrives much better when not grazed. Grazing changes it to the Bouteloua consocies.

The *Andropogon scoparius* evidently represents an earlier stage in the formation than the *Andropogon furcatus* or *Bouteloua oligostachya* consocies. It occurs on the hillsides and also is found as an early stage in the succession on denuded xerophytic areas. The study of secondary succession would lead also to the belief that *Muhlenbergia gracillima* is only a stage, for here it is replaced repeatedly by *Bouteloua oligostachya.*

The societies of the formation are, without exception, dominated by species which are among the first to invade new areas. Their presence in the formation is largely due to historical reasons. To this may be added the fact that the consocies which represent the earlier stages, as for example the *Bouteloua hirsuta* consocies, have by far the greater number of societies.

The *Bouteloua oligostachya* consocies represents the ultimate stage of the grass formation and is by far the most widely distributed of any of the consocies of the formation.

This study of the Bouteloua formation was suggested by Professor FREDERIC E. CLEMENTS, under whose direction it has been carried on. To him and also to Professor CHAS. E. BESSEY the writer wishes to express his thanks for many helpful suggestions and criticisms. Thanks are also due to the following persons: Professor F. D. HEALD, for advice and criticism; Professor WM. STRIEBY, for generously giving me use of his laboratory for the determination of water content; and to Professor F. H. LOUD, for meteorological data.

UNIVERSITY OF MISSOURI, COLUMBIA.

CORTINARIUS AS A MYCORHIZA-PRODUCING FUNGUS[1]

C. H. KAUFFMAN.

(WITH ONE FIGURE)

THE study of the mycorhiza problems has received a new impetus during the last six years by the appearance of extensive papers by MACDOUGAL (1), STAHL (2), TUBEUF (3), HILTNER (4), and MÜLLER (5). Considerable evidence has been adduced showing that in the case of the endotrophic mycorhiza the organisms concerned act as purveyors of nitrogen to the symbiont or host with whose roots they are connected (6–7); furthermore, the organisms in some of these cases have been quite exhaustively studied (8–9). On the other hand, the fungi which cause the ectotrophic mycorhiza have not been investigated except in a very few cases.

It is a noticeable fact as one looks over the literature, that the larger part of the work hitherto attempted has been done on a basis of several unknown quantities. One of these is the identity of the fungus which causes the ectotrophic mycorhiza. The earlier writers speak of the fungus as if it were a single species or genus. It was thought for quite a time that the ectotrophic mycorhiza of European trees was due in all cases to the tubers or truffles. WORONIN (10), in 1885, showed that this cannot be true for Finland, where the tubers are not found, but where nevertheless the mycorhiza are abundant. KAMIENSKI(11) also found no truffles in the regions where he studied the mycorhiza of Monotropa. REES (12) was at first inclined to think that Elaphomyces was the cause of the mycorhiza of almost all the trees he examined; later, he himself found mycelium of mycorhiza which differed in structure from that of Elaphomyces.

The fungi whose fruiting forms have been definitely reported as belonging to mycorhizal mycelium are comparatively few. MACDOUGAL (1) gives a list of mycorhizal fungi whose identity has been reported. The list is as follows: Fusisporium, Eurotium, Pythium, Nectria, Celtidia, Elaphomyces, Geaster, Boletus, Tricholoma, Lactarius, and Cortinarius. Of the non-mycelioid forms

[1] Contribution 89 from the Botanical Department of the University of Michigan.

which are known, *Phytomyxa leguminosarum* and Frankia are of course the most prominent. It will be seen that the list is remarkably small, especially if we remember that only one or two species is referred to in each case. As we are only concerned with ectotrophic forms, the first four can be omitted in the discussion, and if we consider the evidence on which the symbiotic connection of the remainder is based, we find the actual list even smaller.

In the case of the Boleti, WORONIN (**10**), after declaring the tubers out of the question, says: "Vielleicht gehört die hiesige Mycorhiza einem anderen, ebenfalls unterirdischen Pilze an, dies will ich nicht bestreiten, bin aber vielmehr geneigt anzunehmen, dass die oben angeführten Boleten mit der Mycorhizen zusammenhängen." It seems that WORONIN himself was not very certain of the connection. Elaphomyces was very exhaustively studied by REES (**11**), who showed that it is undoubtedly connected with the pines in localities where the truffle occurs. Two species of Geaster, *G. fimbriatus* and *G. fornicatus*, were shown by NOACK (**13**) to be attached to the roots of the spruce and pine.

When we come to a consideration of the agarics our knowledge is meager indeed. Only one investigator, NOACK (**13**), in 1889, has concerned himself with them. He found that five species of this group were apparently mycorhiza-producers on the forest trees of the locality where he made his observations. Two were Tricholomas; one a Lactarius; and three were Cortinarii. He merely makes the bare statement that they are connected with the rootlets by their mycelial strands, which he could easily make out. It is very probable that his observations are correct.

It seems to be appreciated that we need some investigation to determine what fungus we are dealing with, so that problems which have to do with the physiological side of mycorhiza may be undertaken more intelligently; for it is just as likely that knowledge concerning the fungus and its life history may lead to an understanding of the relation of the two organisms as a knowledge of the tree would. It seemed worth while, therefore, to report the identity of any such mycorhizal fungi whenever the evidence seemed sufficient to make it acceptable.

OBSERVATIONS ON **Cortinarius rubipes,** sp. nov.[2]

In a previous paper (**14**) I pointed out that the members of the genus Cortinarius were so constantly found in limited areas, and some species in such close proximity to certain trees, that it seemed likely that there was some connection. This last summer an effort was made to find out to what extent this might be true. The season was wet during the early summer, and although one finds few Cortinarii as a rule before August, several did occur, and one of

FIG. 1.—*Cortinarius rubipes*, sp. nov.—Left hand sporophores show the mass of rootlets and humus with strands of mycelium projecting above; right hand individual shows the roots with the short mycorhizal branches and the mycelial strands which are attached to the base of the stipe.—Photographed by the writer.

these proved to be favorable for my purpose. It not only showed beautifully its connection with the tree roots, but turned out to be an undescribed species of Cortinarius.

It was found July 4, 1905, on the south slope of a small ravine along the Huron River, near Ann Arbor, in a layer of humus and forest leaves. This species, as is indeed true of some other fleshy fungi, is characterized by its brick-red mycelial strands and stem. By removing the surface soil it was possible to see the brick-red strands intertwining with the rootlets apparently in all directions.

[2] For description in full, see 8th Report Mich. Acad. Sci. 1906.

But it was soon found that the reddish network extended along definite paths. Beginning with a tiny rootlet, the fungus was followed to a rather large root, apparently growing from a hickory. On examination, however, it was found that the mycorhiza-bearing root passed the hickory, and that all the roots of the hickory examined were devoid of a colored mycorhizal fungus. On the other hand, the root in question was now easily traced to a clump of red oaks, of second year growth, which were distant at least 54^{dm} from the starting point. Besides the hickory, the roots of a Crataegus which crossed the oak roots were likewise devoid of the fungus in question.

The red strands were attached only to the small rootlets, and where the roots extended below the black soil into the yellow subsoil the mycorhiza gradually disappeared, facts which were known to FRANK, STAHL, and others. The leaf mold along with the remains of last year's leaves forms a thin covering beneath which the young buttons of the fungus are started.

About twenty paces down the slope, another troop of the same species of Cortinarius was found. These came up only 30^{cm} away from a fine young sugar maple and close to one of its main roots. Expecting that they were probably attached to the roots of an oak a short distance away, I dug down carefully and found to my surprise that the strands which were very luxuriant here were attached to the rootlets of the sugar maple; even the small roots growing directly from the base of the trunk were thickly beset by the strands. The sporophores were loosened and the attachment of the strands followed from the stipe to the rootlets and thence to the tree. Several days later on visiting the same hill, two more sporophores were found on the north slope of the hill, again with the characteristic strands, and connected with a red oak.

I had to leave Ann Arbor at this time, and not until I came back in September did I have any further opportunity to make observations. On October 30 the slope was dug over for a considerable area around the original habitat of the Cortinarius in question. The roots of the same maple were found to be hung with the reddish strands in all directions, just as luxuriant apparently as in the early summer. Here, also, other roots crossing or intertwining with the maple roots—with one exception—were not affected by the fungus.

An ash, basswood, and white oak were examined, but no trace of the fungus found. About 27^{dm} from the sugar maple, it was found that some of the strands were apparently attached to a different root. Following this up to a clump of red oaks about 54^{dm} away, I was again surprised to find that the oak roots in this case were not connected with the fungus at all, but that the root which was followed —which did not have the appearance of an oak root—belonged to a large *Celastrus scandens* which wound around one of the oaks. It was clear that we had another symbiont connected with the fungus.

Discussion

It may be well here to call attention to the following points which have been brought out: (*a*) that *Cortinarius rubipes* (for so we will call it) is connected with three forest symbionts belonging to different families; (*b*) that it is apparently selective in the sense that the specific character of the symbiont does not necessarily attract it; (*c*) that one of the symbionts is a maple.

Noack (**12**), who has been the only investigator of the agarics as producers of mycorhiza, thinks he has connected *Tricholoma terreum* with both beech and fir, and *Lactarius piperatus* with beech and oak. My own observations seem to show that it is undoubtedly a fact that one fungus may be attached to trees of very different families. In the case of *Celastrus scandens* no fruit bodies were seen, but there can hardly be a doubt that it was the mycelium of the same species.

It is rather unexpected to find that the same tree species when exposed to the fungus does not always become associated with it. It is evident that the mycorhizal fungus may attach itself to very different hosts, dependent for its initial attachment on certain environmental factors.

The maples of Europe are reported as seldom forming mycorhiza (**2**). The roots of the sugar maple mentioned above were carefully examined with a lens, and also under the microscope, and mycorhiza seemed to be everywhere abundant on the smaller rootlets. How generally they occur on our maples is not known, as hardly any work has been done in this line in our country.

With regard to the kind of mycorhiza involved, there is of course

no uncertainty. Some of the strands and the connected rootlets were fixed and imbedded, and sections were made to determine the more intimate relations of the two organs. When stained rather deeply by fuchsin and gentian-violet the connection could be easily made out. It is clearly a true ectotrophic mycorhiza. There is a close-lying layer of parallel hyphae which surrounds the rootlet, and, in all but the youngest rootlets, branches of this layer penetrate the root and form a close intercellular tissue exactly as figured by FRANK (**13**). The cells of the root at this time seem to contain little protoplasm and occasionally hyphal threads are seen to cross the cells of the cortical layer farther in. In the youngest roots no intercellular tissue appears to be present.

It would seem that there must be some close physiological relation; FRANK indeed thought he had demonstrated it. At the present time, however, nothing definite is agreed upon. To attempt in some measure to solve this question, experiments are now under way with the mycelium of the above-mentioned mushroom. One fact may have some bearing on the problem; the species of the genus Cortinarius develop relatively slowly. The writer has never been able to bring buttons into the house and develop them there, as is possible with Amanitas and Volvaria. For some reason they seem to have lost the vigor necessary to this end. It may be that the explanation of this is found in that a part of their food supply is cut off, and that the tree really supplies some of the necessaries for the full development of the sporophore.

Let it not be supposed that all Cortinarii are mycorhiza-formers, at least normally. *Cortinarius armillatus*, for example, although very partial to *Tsuga canadensis*, is usually found among rotten logs or leaf-mold near this tree, and is probably a saprophyte; on the other hand, it has been found growing out of a cleft at the base of one of these hemlock trees. It seems quite likely, however, that a good many Cortinarii are in symbiotic connection in the manner of the one described in this paper. During several seasons' observations, I have found *C. squammulosus*, *C. bolaris*, and *C. cinnabarinus* again and again in places which would indicate some relation to one kind of tree. *C. cinnabarinus* seems to prefer the oak, the other two the beech. NOACK (**12**) has shown the connection of *Cortinarius callisteus*

with the beech, *C. caerulescens* with the beech, and *C. fulmineus* with the oak. Others will no doubt be added to the list as soon as observers enter this interesting field.

UNIVERSITY OF MICHIGAN, ANN ARBOR.

LITERATURE CITED.

1. MACDOUGAL, D. T., Symbiotic saprophytism. Annals of Botany **13**:1.1899.
2. STAHL, E., Der Sinn der Mycorhizenbildung. Jahrb. Wiss. Bot. **34**:539. 1900.
3. TUBEUF, K., Beiträge zur Mycorhizafrage. Naturwiss. Zeitsch. Land. Forstwirts. **1**:Feb. 1903.
4. HILTNER, L., Beiträge der Mycorhizafrage. Idem **1**:Jan. 1903.
5. MÜLLER, P. E., Über das Verhältniss der Bergkiefer zur Fichte in den Jutländischen Heideculturen. Idem **1**:Aug. & Oct. 1903.
6. HELLRIEGEL H. & WILFARTH H., Untersuchungen über die Stickstoffernährung. Ber. Deutsch. Bot. Gesells. **7**:138 and footnote. 1889.
7. NOBBE & HILTNER, Die endotrophe Mycorhiza von Podocarpus und ihre physiologische Bedeutung. Landwirts. Versuchsst. 51. 1899.
8. ATKINSON, G. F., Contribution to the biology of the organism causing leguminous tubercles. Bot. Gaz. **18**:157, 226, 257. 1893; and literature quoted.
9. SHIBATA, K., Cytologische Studien über die Endotrophen Mycorhizen. Jahrb. Wiss. Bot. **37**:643. 1902.
10. WORONIN, M., Über die Pilzwurzel von B. Frank. Ber. Deutsch. Bot. Gesells. **3**:205. 1885.
11. REES, M., Über Elaphomyces und sonstige Wurzelpilze. Ber. Deutsch. Bot. Gesells. **3**:294. 1885.
——— Über den Parasitismus von *Elaphomyces granulatus*. Bot. Zeit. **38**:729. 1880.
12. NOACK, Über Mycorhizenbildende Pilze. Bot. Zeit. **47**:389. 1889.
13. FRANK, B., Ber. Deutsch. Bot. Gesells. **3**:*pl. 10*.
14. KAUFFMAN, C. H., Bull. Torr. Bot. Club **32**:301. 1905.

A NEW FUNGUS OF ECONOMIC IMPORTANCE.

RALPH E. SMITH AND ELIZABETH H. SMITH.

(WITH THREE FIGURES)

AMONG the subjects of investigation by the California Agricultural Experiment Station, that of a destructive rotting of lemons occurring in southern California is one of the most important. The cause and means of control of this rot have been a complete mystery to the handlers of lemons, and the fact that the trouble has been found to be due to a fungus representing not only a new species, but a well-defined new genus, makes the case one of peculiar interest.

The rot in question has been called the "brown rot," distinguishing it from the "blue mould," or Penicillium rot, the commonest form of Citrus decay. The latter has been known since time immemorial, but with the best class of lemon shippers is not usually a great pest. Lemons affected by Penicillium are almost invariably those which have become bruised in handling or subjected to improper conditions. With fruit properly handled, cases of blue mould are only occasional. In these the affected lemon decays and becomes covered with the dusty fungus, finally collapsing into a slimy mass, without infecting the other fruit, even though they be covered with the spores. A Penicillium-affected lemon in the midst of a box does not usually infect the other fruit about it in the least when proper conditions are maintained.

Within the past few years a new and much more serious form of rot has been detected by the lemon growers and shippers. In lemons which had been picked, washed, and stored for curing, it was found that a rot developed which spread rapidly by contact through the fruit, soon involving the entire box if left undisturbed. In appearance the affected lemons are characteristic and easily distinguished from those affected by blue mould, though the latter fungus follows rapidly on the other and soon covers the decaying fruit. Particularly characteristic is the odor of lemons affected by brown rot, a peculiar rancid smell by which an experienced person can detect one affected lemon in a large amount of fruit. This

odor has, in fact, come to be the infallible test for brown rot in the lemon curing houses, readily distinguishing the trouble from all other forms of decay. The rapid spread in the box by contact, and the appearance of affected fruit, are also very characteristic, though the latter is soon disguised by Penicillium, and the former feature is even more true with a rot caused by Sclerotinia.

When brown rot first appeared in the packing houses, search was made in the orchard to locate the origin of the trouble, with the result that even upon the tree affected lemons could be found. This was only the case during the wet season, which, in fact, is the only time when the rot is troublesome.

It is not the purpose of the present article to describe this trouble at length, but simply to place on record a description of the fungus and sufficient characterization of its effects to serve to identify this form of lemon decay. Lemons affected on the tree show a brownish, discolored area on the side or end, free from any mould or appearance of fungus, and without any decided softening of the rind, but gradually spreading and soon involving the whole lemon. The fruit keeps its size, shape, and solidity, even when totally affected, before which time it usually drops to the ground. The orchard occurrence is not generally abundant except in wet, warm spring weather or under like conditions. Affected lemons have a peculiar characteristic odor, and are readily identified by one familiar with the disease.

Lemons are usually picked quite green, washed in a machine consisting of a tank of water with revolving brushes, and then stored in boxes for several weeks to cure. At times of abundant prevalence of rot, great loss is experienced in such stored fruit. In lemons apparently sound when put away, affected spots develop on individuals here and there in the boxes. These are soon involved, and also all those which lie in contact with them. These again spread the trouble, and an extremely virulent decay results. Lemons affected in this way have the appearance above described, except that a rather delicate, white mycelium develops on the surface and grows from lemon to lemon, causing the contact infection. The trouble never spreads in the mass of stored fruit except by actual contact of the healthy lemon with an affected spot. When a large

amount of fruit becomes affected the characteristic odor is very pronounced. Penicillium follows rapidly and covers the affected lemons.

With reference particularly to the cause of the trouble, the fungus, which comes out on affected fruit in moist air and spreads from

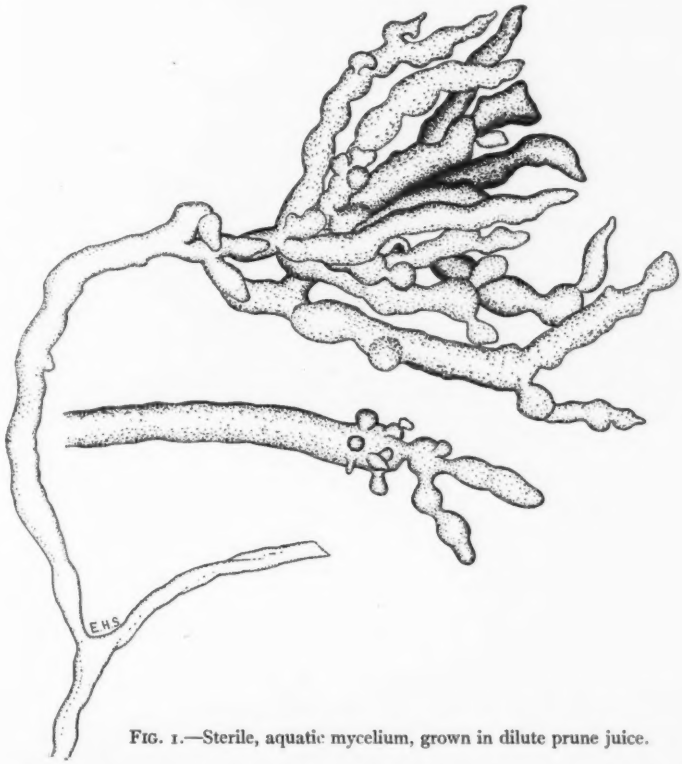


FIG. 1.—Sterile, aquatic mycelium, grown in dilute prune juice.

lemon to lemon, consists of a sterile mycelium, composed of large branching, mostly continuous filaments. If an affected lemon be placed in water for several hours, this mycelium develops more richly upon the surface, forming a slimy, Saprolegnia-like growth. The fungus quickly reaches the fibrous core of the lemon, bits of which soaked in water are soon surrounded with a luxuriant growth

On dry or simply moist media (gelatin, bread, etc.) little or no growth can be obtained. In dilute prune juice the fungus grows with extreme vigor, forming a luxuriant mycelium of very large, branching, continuous filaments (*fig. 1*). Such growths are entirely sterile or nearly so. Occasionally there are produced a few large, ovate, terminal conidia or sporangia, of the phycomycete type, which germinate directly in water or form swarm-spores. Numerous cultures in various liquid media have developed nothing but the mycelium and occasional spores of this kind. This fungus is nearly sterile under such conditions, and entirely so on affected lemons in the air, though with extreme vegetative vigor. Cultures of pieces of affected lemon in pure water, kept for a long time, usually develop nothing but mycelium, though occasionally conidia or sporangia are produced to some extent. Bits of this sterile mycelium placed on sound lemons in a moist chamber produce infection and characteristic rot. Lemons soaked in water, into

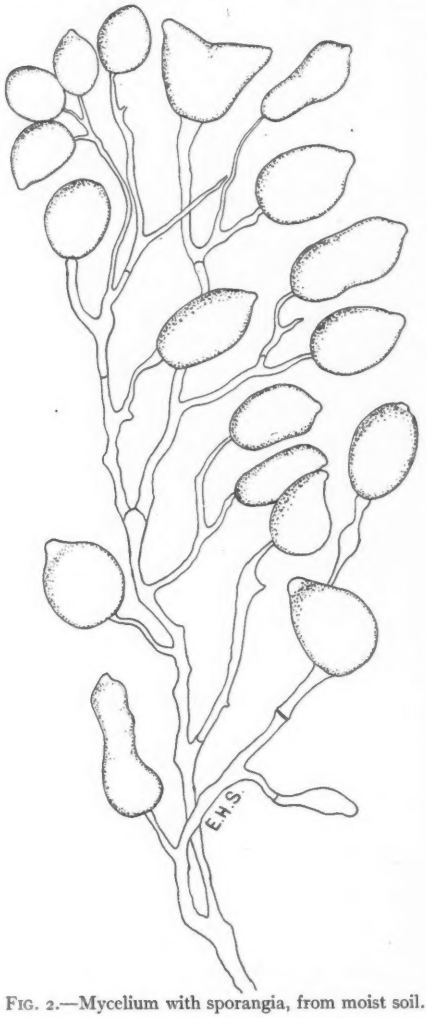


FIG. 2.—Mycelium with sporangia, from moist soil.

which a sterile culture of the fungus has been mixed, also become infected.

Affected lemons placed on moist soil (as in nature by falling from the tree) produce a visible mycelium upon the surface and make such ground highly infectious to sound fruit laid upon the surface. In soil thus inoculated the characteristic spore stage of the fungus has been found. This is also readily produced on wet filter paper

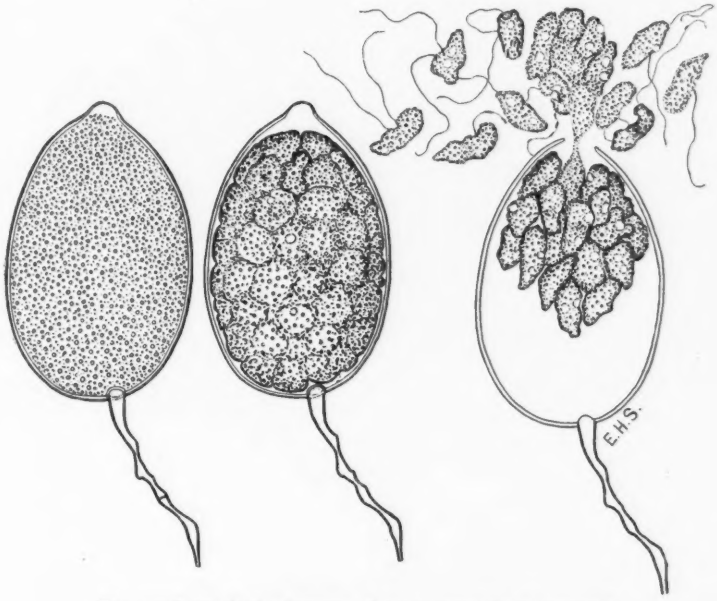


FIG. 3.—Stages in development of swarmspores from sporangia.

in the bottom of a moist chamber containing an affected lemon. Upon an extremely delicate, fine, septate, branching mycelium, very numerous, terminal sporangia are produced (*fig. 2*), much as in Pythium under similar conditions. These sporangia differ, however, from those of the latter genus, in producing swarmspores by direct internal division, behaving in this respect like those of Phytophthora, which they also resemble in appearance (*fig. 3*). The appended description gives further details. These swarm-

spores are extremely infectious to sound, green fruit in all stages of development.

Lemons on the tree become infected during the rainy winter and spring months, almost entirely on the lower part of the trees (which are allowed to branch close to the ground), and in the wettest part of the orchard. The fungus at all times shows a very decided moisture requirement for its development. Infection takes place by swarmspores from the soil, both on the tree and in the washing tank, in the latter case by the orchard dirt, dust, leaves, and other sediment which accumulates in the water.

The writers have given much consideration to the generic relations of this fungus, particularly as to whether it is sufficiently distinct from Pythium and from DE BARY'S Pythiopsis. It is remarkable for the connection which it presents between the Phycomycetes of this nature. While similar to Pythium in habit, except as to its peculiar parasitism on the lemon, this species is definitely excluded from that genus by its internal formation of swarmspores. We have felt considerable hesitancy in separating this form from Pythiopsis, on account of the similarity in swarmspore formation; the latter, however, being founded on a species of such different habit, an entomophthorous form of the Saprolegnieae, and being practically unknown save from the original description, we feel justified in proposing a new genus for our species. It is particularly of interest as being more exactly intermediate between the Saprolegnieae and Peronosporeae than either Pythium or Pythiopsis, and also forming a close transition from Pythium to Phytophthora, having the swarmspore formation and something of the parasitic tendency of the latter. In brief, Pythiacystis has the soil habit of Pythium, the aquatic habit of the same and of the Saprolegnieae (including Pythiopsis) except for its usual sterility under such conditions, the sporangia formation of Pythium, the swarmspore formation of Pythiopsis and Phytophthora, and parasitic activity intermediate between Pythium and Phytophthora.

No indication of sexual reproduction has been observed in the large amount of material and numerous cultures examined.

An Experiment Station bulletin on the nature and control of this fungus will be issued in due time.

Pythiacystis Smith & Smith, n. gen.

Parasitic on living plants, or saprophytic with abundant moisture. Fertile mycelium delicate, septate, with numerous, terminal, sympodially developed sporangia. Aquatic mycelium typically sterile, with occasional conidia or sporangia. Filaments very large and vigorous, continuous, much branched.

Sporangia typically rounded or ovate, dividing internally into biciliate swarmspores which immediately become motile and emerge from a terminal opening.

Conidia similar to sporangia, germinating directly by a germ tube.

Sexual reproduction not observed.

Differs from Pythium in mode of swarmspore formation, and from Pythiopsis in habit. Closely intermediate between Saprolegnieae and Peronosporeae.

Pythiacystis citrophthora Smith & Smith, n. sp.—Parasitic on lemons, and occasionally other Citrus fruits, causing decay of green fruit on the tree and in the storehouse. Mycelium in affected fruit sterile, inhabiting rind and fibrous portions. Internal, except in moist air. Mycelium in water or nutrient liquids very vigorous, usually sterile, or occasionally with conidia or sporangia. Fruiting stage found typically in moist soil, in contact with affected fruit. Sporangia ovate or lemon-shaped, sometimes rounded, considerably elongated, or double, with terminal protuberance; $20\times30\mu$ to $60\times90\mu$, av. $35\times50\ \mu$. Produced in great abundance under favorable conditions. In water dividing quickly by internal division into 5 to 40 (usually about 30) swarmspores, which are immediately set free and discharged through a terminal pore.

Swarmspores 10 to 16 μ in diameter, at first elongated, becoming rounded; with two lateral cilia 30 to 40 μ in length. Actively motile when discharged, soon coming to rest and germinating.

Fungus abundant in winter and spring in southern California lemon orchards and packing houses, causing serious losses.

UNIVERSITY OF CALIFORNIA, BERKELEY.

CURRENT LITERATURE.

BOOK REVIEWS.

American fossil cycads.[1]

SINCE 1898 DR. WIELAND has been investigating the wonderful American display of fossil cycadean forms, usually referred to now as the Bennettitales. The investigation has demanded an unusual amount of patience and hard work in making the necessary collections and sections. The student of living plants has no adequate conception of the labor involved in obtaining valuable results from sectioning fossil material. The result of all this work now appears in a bulky memoir published by the Carnegie Institution. It is a veritable mine of information in reference to Bennettitales, a mine that will be worked by botanists for a long time to come. To present the results here would be to write another book. They are not essentially new, but they are so much more complete and more finely illustrated than ever before that the student of gymnosperms must always consult this volume.

The contents may be outlined by giving the chapter headings as follows: discoveries and collections, preservation and external characters, on the methods of section cutting, trunk structure, foliage, ovulate cones, bisporangiate axes, young fructifications, existing and fossil cycads compared, fern ancestry and angiosperm analogies.

The author is to be congratulated upon the amount of good work that he has accomplished and upon the fine and permanent form in which it has appeared. Morphologists can now lay hold of this material as they never could before, and organize it for general use.—J. M. C.

MINOR NOTICES.

Reproduction.—Under the title "multiplication and sexuality in plants," KÜSTER[2] has published some expanded lectures which were given in January and February of this year and constituted "an advance course for teachers." Vegetative multiplication is first considered in the higher plants, then in the lower. Sexual reproduction is treated historically, and then taken up from the standpoint of its evolution, the lower forms being treated first. The general problems discussed are: sexual affinity, hybridization, polyspermy, parthenogenesis, apogamy, apospory, and distribution of sexes. The book closes with remarks on theories of reproduction and sexuality. It is a convenient, compact, and reliable compendium of the subject.—CHARLES J. CHAMBERLAIN.

[1] WIELAND, G. R., American fossil cycads. pp. 296. *pls.* 50. *figs.* 138. Carnegie Institution. 1906.

[2] KÜSTER, ERNST, Vermehrung und Sexualität bei den Pflanzen. 8vo. p. vi+120. *figs.* 38. Leipzig: B. C. Teubner. 1906. *M* 1.25.

Leaflets on Philippine botany.—Under this title A. D. E. ELMER proposes to issue in serial form articles on Philippine plants, both scientific and economic, printed in English, Latin, German, or French. This publication will appear at irregular intervals, at a subscription price of $1\frac{3}{4}$ cents per page, and may be obtained by addressing the editor at Manila. The first issue is a paper of 41 pages entitled *Philippine Rubiaceae*, by the editor, containing 150 species, of which 45 are new, representing 42 genera.—J. M. C.

Das Pflanzenreich.[3]—Part 26 contains the Droseraceae by L. DIELS. Drosophyllum, Dionaea, and Aldrovanda are regarded as monotypic genera; while Drosera is credited with 84 species, 5 of which are new. A very full discussion of structure and range precedes the synopsis.—J. M. C.

Pflanzenfamilien.[4]—Part 224 includes the completion of the Spiridentaceae, the Lepyrodontaceae, and the Pleurophascaceae, and a portion of the Neckeraceae, all by V. F. BROTHERUS. Part 225 continues the Ascolichenes by A. ZAHLBRUCKNER.—J. M. C.

NOTES FOR STUDENTS.

Revelations of the ultramicroscope.—GAIDUKOV has been seeing previously invisible things by means of SEIDENTOPF'S ultramicroscope, and hastens to communicate them in two preliminary papers.[5] After mastering the rather difficult technique and the sources of error, he began by observing the expressed contents of a Vaucheria filament, but later found that it was possible to observe the contents *in situ*. He saw the ultramicroscopic particles of plasma and chlorophyll, the former white and blue, the latter red and green—colors whose significance is unknown as yet for lack of sufficient physical investigation of the instrument. He watched the collision of plasma particles with structureless oil drops and their recoil, and the like collisions of chlorophyll particles and their disappearance in the oil, in which the number of red and green chlorophyll granules steadily increased. This appears to be actually the formation of a colloidal solution of chlorophyll in oil—an oleosol.

In examining a living filament he found that the protoplasm occupied a much greater space than appears with ordinary illumination, only a very small part of the filament being optically empty. In the chloroplasts of Mesocarpus, roundish or stellate flecks of chlorophyll particles are distributed through the stroma, whose structure is like that of the protoplasm; there is no indication of the solution of chlorophyll in oil droplets lying in the stroma—a widely accepted notion.

---

[3] ENGLER, A., Das Pflanzenreich. 26 Heft. Droseraceae von L. DIELS. pp. 136. *figs. 40 (286), map 1.* Leipzig: Wilhelm Engelmann. 1906. *M* 6.80.

[4] ENGLER, A. und PRANTL, K., Die natürlichen Pflanzenfamilien. Lieferungen 224 and 225. Leipzig: Wilhelm Engelmann. 1906.

[5] GAIDUKOV, N., Untersuchungen mit Hilfe des Ultramikroskopes nach Seidentopf. Ber. Deutsch. Bot. Gesells. **24**: 107–112, 155–157. 1906.

The nucleus of Tradescantia appears to have a structure like protoplasm, but much more compact.

Bending movements of Oscillaria are accompanied by wave-like movements of particles in the cells; and the longitudinal movements by a streaming of particles on the surface in a direction opposite to that of the motion of the filament. These particles pass off into the water when they reach the end of the filament.

Ultramicroscopic organisms in figure-of-8 forms, and colonies in form like certain flagellates, similar to the organisms already described by RAEHLMANN, were found in every preparation.

Protoplasmic movements have been seen in all organisms investigated, and the ordinary rotation and streaming is by no means the simple flow it seems to be, but is probably initiated by a complex motion of the ultramicroscopic particles (ultramicrons) of the protoplasm, whose structure seems identical with that of colloidal solutions as determined by ZSIGMONDY with the instrument. The first movement, indeed, may be what has long been known as the Brownian movement, once so carefully distinguished from the "vital" ones as "purely physical."

In plasmolysis GAIDUKOV has seen the protoplasmic particles move from the periphery toward the center of the cell, changing shape at the same time from round to vermicular, while in the chloroplast simultaneously the vermicular chlorophyll particles creep out upon the surface. In Flagellatae there is a vigorous movement of particles in the region of the cilia and below the mouth opening, before the gross movements begin.

Whereas in chlorophyllose cells the cell wall is optically empty (*leer*), enabling one to see the cell contents clearly, the wall of bacteria and fungi has so complex a structure that nothing can be seen through it. Yet the purple bacteria which also work photosynthesis have a wall optically empty. These facts are believed to be related to the necessity for transparence to light in photosynthetic cells.—C. R. B.

Araucarieae.—A. C. SEWARD and SIBILLE O. FORD have published the results of a study of the Araucarieae.[6] The two living genera representing the group, Agathis and Araucaria, have long stood somewhat stiffly apart from other Coniferales, not only on account of the known facts in reference to them, but chiefly, perhaps, on account of lack of knowledge. The authors have marshalled our knowledge of extinct and living forms in this memoir; and however opinions may differ as to their conclusions, there can be only one opinion as to the value of the work. The subject is presented under the following captions: distribution, generic diagnosis, seedlings, stem anatomy, roots, leaves, leaf-traces, reproductive shoots, fossil Araucarieae, and phylogenetic considerations and conclusion. The details are too numerous to be included in a review, but the conclusions are too important to be passed over lightly.

[6] SEWARD, A. C. and FORD, SIBILLE, O., The Araucarieae, recent and extinct Phil. Trans. Roy. Soc. London. B. **198**: 305–411. *pls. 23–24. figs. 28.* 1906.

In general, the memoir is a contention that the recent brilliant work which has knit together cycads and Filicales has developed the too sweeping conclusion that all gymnosperms have the same phylogenetic connection; that the old view suggesting a connection between conifers and lycopods deserves more attention than it has been receiving; and that at least the Araucarieae strongly suggest a lycopod origin. It is urged upon paleobotanical evidence that the Araucarieae are the most primitive of Coniferales, certainly more primitive than the Abietineae; and that this testimony from history is supported by numerous evidences of relatively primitive structures still exhibited by Agathis and Araucaria. The difficult question of the Cordaitales, which seem to combine characters of Cycadales and Coniferales and so necessitate a common phylogeny, is disposed of by minimizing their resemblances to the latter, at least to the Araucarieae. It must be remarked that the authors repeatedly emphasize the fact that they are dealing only with the Araucarieae, and that it does not affect their main contention whether the other Coniferales are related to a filicinean ancestry through the Cordaitales or not. In developing the differences between the Araucarieae and other Coniferales, they have been so impressed by their importance that they have suggested a group *Araucariales*, coordinate with Coniferales, Cycadales, etc. For this group, at least, they claim a lycopod ancestry, through some such form as Lepidocarpon, emphasizing the seed-like sporangia recently described by SCOTT in that genus.

The authors are to be congratulated upon a very fair statement of their case, a statement which dodges none of the difficulties, and which really does not claim very much more than that an almost abandoned hypothesis must not be neglected.

A very interesting appendix to this memoir may be obtained by reading the report[7] of two recent meetings of the Linnean Society, at which various views as to the origin of gymnosperms were presented and combated by English students of the group.—J. M. C.

Items of taxonomic interest.—N. L. BRITTON (Bull. N. Y. Bot. Gard. **4**:115–127, 137–143. 1906) describes new species of Bahama plants under Coccolobis, Caesalpinia, Canavalia, Hibiscus, Heliotropium (2), Lantana (2), Cestrum, Stemmodontia, Anastraphia, Marsilea, Dondia, Cassia, Maytenus, Myroxylon, Opuntia, Limnanthemum, Metastelma, Aster.—W. H. BLANCHARD (Torreya **6**:147–149. 1906) has described 2 new species of Rubus (dewberries) from New England.—H. D. HOUSE (*idem* 150) has described a new Convolvulus from Georgia.—H. A. GLEASON (Bull. Torr. Bot. Club **33**:387–396. 1906) has revised the pedunculate species of Trillium, defining 19 species, 3 of which are new.—H. D. HOUSE (Rhodora **8**:117–122. 1906) has described the violets and violet hybrids of the District of Columbia and vicinity, recognizing 26 species, and describing 8 new hybrids.—M. L. FERNALD (*idem* 126–130) has described new species of Cyperus (2) and Eleocharis from Eastern North America.

[7] New Phytol. **5**:68–76, 141–148. 1906.

—E. B. COPELAND (Philippine Jour. Sci. **1**:143–166. *pls. 28*. 1906) has described 47 new species and 2 new genera (*Acrosorus* and *Thayeria*) of Philippine ferns. —SPENCER LE M. MOORE (Jour. Botany **44**:217–224. 1906) has described 2 new genera of Acanthaceae from Madagascar, *Melittacanthus* and *Amphiestes*.—BUNZO HAYATA (Jour. Linn. Soc. Bot. **37**:330. *pl. 16*. 1906) has described a new genus (*Taiwania*) of conifers from the Island of Formosa, belonging to the Taxodieae and nearest to Cunninghamia.—EDITH M. FARR (Ottawa Nat. **20**:105–111. 1906) has described new species from the Canadian Rockies and Selkirks under Pachystima (4), Arnica, Hieracium, Dryas, and Ranunculus.— O. STAPF (Kew Bulletin 1906 : 204) has published a new genus (*Diandrolyra*) of grasses whose native country is unknown.— O. E. JENNINGS (Annals Carnegie Mus. **3** : 480–485. 1906) has published new species under Kneiffia and Ibidium (Spiranthes) from Pennsylvania.—V. F. BROTHERUS (Hedwigia **45** : 271. 1906) has described a new genus (*Uleobryum*) of Pottiaceae from Peru.—F. LAMSON-SCRIBNER (Rhodora **8** : 137–146. 1906) has included in a newly named genus (*Sphenopholis*) the grasses that have been referred for many years to *Eatonia* Raf., recognizing 7 species.—W. H. BLANCHARD (*idem* 146–157) has described 5 new blackberries (Rubus) from Maine.—R. SCHLECHTER (Engler's Bot. Jahrb. **38** : 137–143. 1906) has described two new African genera (*Afrothismia* and *Oxygyne*) of Burmanniaceae.—J. C. ARTHUR and F. D. KERN (Bull. Torr. Bot. Club **33** : 403–438. 1906), in a revision of the N. Am. species of Peridermium, recognize 30 species, 10 of which are described as new.—K. K. MACKENZIE (*idem* 439–443) has described 4 new species of Carex.—LEROY ABRAMS (*idem* 445–446) has described 2 new southwestern species of Pentstemon.—J. M. C.

Japanese Experiment Station Bulletin.—A new departure in experiment station publications had been inaugurated by Professor HOZAI of the Imperial Central Agricultural Experiment Station of Tokio. In order to make the results of work carried on in the experiment stations of Japan accessible to investigators of other countries, a periodical Bulletin will be issued in which all work that may be of general interest will be published. The experimental system of Japan comprises 47 stations, whose work will in large part become available to the world through the publication of this Bulletin, printed partly in English and partly in German. The first number[8] contains 11 articles, some of which are briefly noted here to show the scope of the publication. S. MACHIDA reports on the influence of dilute solutions (0.3%) of Ca and Mg salts on the putrefactive action of bacteria. The rate of putrefaction was determined by the quantity of NH_3 formed in urine and in pepton solutions to which the salts had been added. It was found that the Ca-salts retard putrefaction, while Mg-salts favor the process.

Several articles of agronomic interest are given by G. DAIKUHARA on the correction of an unfavorable ratio of lime to magnesia, also on the lime factor

[8] The Bulletin of the Imperial Central Agricultural Experiment Station, Japan. Vol. I. No. 1. pp. 94. *pls. 13*. Nishigahara, Tokio. December 1905.

for the tobacco plant, and on the application of magnesia in the form of magnesium sulfate for the rice plant. UYEDA gives an extended account of a new phytopathological bacterium (*Bacillus Nicotianae*) which produces a serious disease known as stem-rot and black-leg of tobacco. HORI gives an account of a smut on the cultivated bamboo. The fungus attacks the young internodes of growing branches, and as it may infect these at any time during the growing season, whole forests of bamboo often become infected. As the bamboo furnishes material for building as well as for household utensils and fences, the damage thus caused is considerable. The fungus is referred to *Ustilago Shiraiana* P. Henn.—H. HASSELBRING.

Respiratory enzymes.—PALLADIN announces his adherence to the theory of BACH and CHODAT, that normal respiration depends upon the presence of 1) oxidizable substance and 2) two enzymes, whose mixture was formerly designated oxidase, *a*) oxygenase, which has, attached to various radicals, the characteristic peroxid or hydroperoxid group O·O or O·OH and serves to transfer O_2, and *b*) peroxydase, which is a catalyser and renders active the oxygenase. When oxidative processes do not occur it is because one or two of the three are wanting. The less stable oxygenases, and those which with water quickly become hydroperoxids, are used up promptly, giving rise to some of the respiratory CO_2; so that often tests do not show any "oxidase" present in plant parts; but the peroxidases, which are very stable, can always be found.

From his researches PALLADIN concludes[9] that the prevalence of one or the other enzyme is connected with the stage of development of the plant. For anaerobic respiration prevails in embryonal organs and in lower plants, which alone are capable of anaerobic life. In the embryonal stage oxygenase is at a minimum, increasing with the passage into active life, and diminishing in organs which have ceased to grow.

Miss KRASNOSSELSKY,[10] working under PALLADIN'S direction, finds in frozen onions and their sap no oxygenase, but peroxydases whose quantity increases with respiratory activity, if H_2O_2 be supplied, and continues to do so even when respiration falls. Katalase, however, is present in the sap after the freezing.

These researches are more and more justifying the opinion that the origin of "respiratory" CO_2 is very complex, and that more than one catalyser is taking part in the dissociation.—C. R. B.

Ancient history of ferns.—ARBER[11] has brought together the recent development of knowledge in reference to the history of ferns in a short paper that brings

[9] PALLADIN, W., Bildung der verschiedenen Atmungsenzyme in Abhängigkeit von dem Entwicklungstadium des Pflanzen. Ber. Deutsch. Bot. Gesells. **24**:97–107. 1906.

[10] KRASNOSSELSKY, T., Bildung der Atmungsenzyme in verletzten Zwiebeln von *Allium Cepa*. Ber. Deutsch. Bot. Gesells. **24**:134–141. 1906.

[11] ARBER, E. A. NEWELL, On the past history of ferns. Annals of Botany **20**: 215–232. 1906.

the important facts well in view, however opinions may differ as to some of the conclusions. It is shown that the fern-like Cycadofilices, later called Pteridosperms, were a dominant group of the Carboniferous; but that the evidence for the existence of ferns in the modern sense is at present very uncertain. For any Carboniferous fern-like plants that may prove to be true ferns the author suggests the name *Primofilices*, since to distinguish among them definite eusporangiate and leptosporangiate habits is impossible. In fact, all the so-called "fructifications" of Paleozoic "marattiaceous ferns" may prove to be the microsporangiate structures of Pteridosperms. Until this is determined, the existence of eusporangiate ferns in the Paleozoic as a dominant group must remain uncertain. This also means that the old question as to whether the eusporangiate or the leptosporangiate type of ferns is the more primitive has lost its apparently sure answer from history. In fact, while the author gets sure evidence of leptosporangiate ferns in the Permian, he does not find similar satisfactory evidence of eusporangiate ferns until the Tertiary; although in both cases he recognizes the possible Paleozoic occurrence. As to the water ferns, the evidence of their existence does not become clear until the Tertiary. The claims for them in the Paleozoic are so much in conflict with all morphological testimony that they have never seemed to be very serious. The general conclusion in reference to the ferns seems to be that while Pteridosperms are a dominant group in the Paleozoic; and the Cycadophyta are one of the dominating groups of the Mesozoic; there is no evidence at present of the dominance of any fern group except that of the leptosporangiates in the Mesozoic and continuing into the present flora.—J. M. C.

Spores of Riccia glauca.—BEER[12] has investigated the development of the spores of *Riccia glauca*, contrasting his results with those of GARBER[13] on *R. natans*, and of LEWIS[14] on *R. crystallina*. The spore mother cells are at first separated by extremely delicate membranes in which no cellulose could be demonstrated, and upon them secondary and tertiary thickening layers are deposited which give pectose-cellulose reactions. The secondary layer becomes more or less mucilaginous, sometimes separating completely from the primary wall, at other times remaining partly adherent and becoming drawn out into strands bridging the space between the primary wall and the tertiary layer. No nutritive material was found between the isolated mother cells, and no non-nucleated reticular resting nucleus was found. The large deep-staining nucleolus consists of a number of deeply chromatic granules embedded in a faintly staining matrix. A long and well-marked spirem thread occurs in the prophase of the division of the mother cell. The reduced number of chromosomes is 7 or 8. In telo-

[12] BEER, RUDOLF, On the development of the spores of *Riccia glauca*. Annals of Botany **20**:275–291. *pls. 21–22.* 1906.

[13] BOT. GAZETTE **37**:161–177. 1904.

[14] BOT. GAZETTE **41**:109–138. 1906.

phase a number of chromatic bodies (presumably derivatives of the chromosomes) are distributed on the linin fibers, and subsequently aggregate to form the lobular nucleolus of the resting nucleus. The first spore wall is cuticularized from a very early period, and within it, at the equatorial rim, a plug of mucilage is deposited. The second spore wall is formed within the first wall, and is also cuticularized; at first it appears homogeneous, but subseqently is composed of three regions. The endospore (pectose and cellulose) is formed late, and is often separated from the second wall by a thin band of dark material.—J. M. C.

Postelsia.[15]—Four years ago the first volume under this title appeared,[16] containing seven papers by members of the Minnesota Seaside Station on the coast of Vancouver. The present volume is printed in the same handsome style, and also contains seven papers as follows: Observations on plant distribution in Renfrew district of Vancouver Island (pp. 1–132. *pls. 1–11*), by C. O. ROSENDAHL; The Conifers of Vancouver Island (pp. 133–212. *pls. 12–15*), by F. K. BUTTERS; Hepaticae of Vancouver Island (pp. 213–235), by ALEXANDER W. EVANS; Some western Helvellineae (pp. 236–244), by D. S. HONE; *Renfrewia parvula*, a new kelp from Vancouver Island (pp. 245–274. *pls. 16–19*), by ROBERT F. GRIGGS; A study of the tide-pools on the west coast of Vancouver Island (pp. 275–304, *pls. 20–25*), by ISABEL HENKEL; Some geological features of the Minnesota Seaside Station (pp. 305–347. *pls. 26–33*), by C. W. HALL.

The paper on plant distribution reaches the conclusion that the pteridophytes are poor in species for so moist a region, that the gymnosperms constitute the great mass of the vegetation, and that the monocotyledons are more important than the dicotyledons. The paper on conifers contains very interesting observations, treats Picea, Tsuga, and Pseudotsuga as sections under Abies, and organizes a key to the northwestern genera on the basis of foliage. *Renfrewia* is a new genus of kelps nearest to Laminaria and Cymathere.—J. M. C.

Synapsis and reduction.—From a study of the pollen mother cells of *Acer platanoides*, *Salomonia biflora*, *Ginkgo biloba*, and *Botrychium obliquum* CARDIFF draws the following conclusions.[17] Synapsis is a constant morphological character of the mother cell, and the unilateral position of the synaptic knot is probably due to gravity. Previous to synapsis the chromatin is in two or more threads which arrange themselves in pairs, longitudinally, and finally fuse during synapsis, but there is not a complete mingling of chromatin substance in the chromatic thread. The thread splits longitudinally in the first mitosis, probably along the line of previous fusion. The chromosomes are of different sizes and do not behave alike at the first mitosis.

---

[15] The year book of the Minnesota Seaside Station. 1906. pp. 364. *pls. 33*. Obtained from Josephine E. Tilden, Univ. Minn., Minneapolis. $2.25.

[16] BOT. GAZETTE **34**:468. 1902.

[17] CARDIFF, I. D., A study of reduction and synapsis. Bull. Torr. Bot. Club **33**:271–306. *pls. 12–15*. 1906.

It is probable that at fertilization there is a nuclear but not a chromatin fusion, and that the paternal and maternal chromatin retain their identity throughout the sporophytic phase, finally fusing, in so far as they fuse at all, during synapsis. If this be true, the two important phenomena of fertilization—stimulus to growth and intermingling of ancestral characters—are widely separated, the stimulus to growth occurring when the nuclei fuse, and the mingling of characters being delayed until synapsis.—CHARLES J. CHAMBERLAIN.

Nutrition of the gymnosperm egg.—Miss STOPES and FUJII[18] have been investigating the nutritive relations of the surrounding tissues to the egg in gymnosperms. As is well known, about the "central cell," and later about the egg, there is organized usually a very distinct jacket of nutritive cells, whose inner walls are conspicuously thickened and pitted. The authors find that the delicate walls of the endosperm cells are pitted in the same way; and that the large pits of the jacket cell-walls are closed by a membrane perforated only by plasmodesmen. This latter fact is the most interesting one of the paper, for it precludes the old notion of nuclear migration or of any transfer of solid material from the jacket cells to the egg. The jacket cells are regarded as glandular, secreting substances for the digestion of the starch and proteid granules stored in the endosperm. The statement is made in the summary that the jacket cells "are considered the phylogenetic homologues of the angiospermic antipodals," a statement evidently based upon their similar function.—J. M. C.

Ecological survey of Northern Michigan.—Under the direction of C. C. ADAMS there has been published[19] the report of an ecological survey conducted by the University Museum of the University of Michigan in 1904. The regions selected were Porcupine Mountains in Ontonagon County, on the south shore of Lake Superior, and Isle Royale, an island near the Canadian shore. Especially significant is the report by A. G. RUTHVEN on the relation of the plants and animals of these regions to their environment. Lines of survey were run across the region examined, in such a way as to include examples of all the representative habitats. These habitats were then examined in as much detail as time permitted, and special attention was given to the relations of the "biota" to its environment. In this study attention was directed particularly to the forces and conditions composing the environment, in order that the dominant forces might be clearly recognized. The results are too numerous and detailed for mention, but the work is unique and extremely suggestive.—J. M. C.

Ecology of algae.—FRITSCH[20] has made a statement of some of the problems

[18] STOPES, M. C. and FUJII, K., The nutritive relations of the surrounding tissues to the archegonia in gymnosperms. Beih. Bot. Centralb. **20**:1–24. *pl. 1.* 1906.

[19] An ecological survey in Northern Michigan. Prepared under the direction of CHAS. C. ADAMS. Publ. in Rep. State Geol. Survey for 1905. pp. 133. *figs. 21.* 1906.

[20] FRITSCH, F. E., Problems in aquatic biology, with special reference to the study of algal periodicity. New Phytol. **5**:149–169. 1906.

connected with the study of algal ecology, and has suggested some means towards their solution. The first problem considered is the determination of what shall constitute a formation, and the contrast with terrestrial formations is made. Suggestions are made as to the significant unit and examples are given. Chief attention, however, is given to algal periodicity, the seasonal variations of algae being much greater than those of terrestrial plants. "In most cases in an aquatic flora a number of dominant forms succeed one another in the course of a year, and after their period of prevalence is past they disappear either suddenly or gradually." Periodicity of algae is either seasonal or irregular, and the factors concerned in both of these cases are discussed. In illustration of his statements, the author discusses the algal flora of a particular pond. The paper is a distinct stimulus to the study of pond life in an effective way.—J. M. C.

Decay of timber.—Following the lines of investigation laid down by HARTIG in his *Zersetzungserscheinungen des Holzes*, BULLER[21] has contributed a further study on the subject of the decay of timber caused by the higher fungi. The form studied is the common *Polyporus squamosus*, which is found on many species of broad-leaved trees. Like other forms of this class, the fungus gains entrance to the tree through wound surfaces. The mycelium progresses more rapidly in a longitudinal direction in the wood, so that the decayed region extends many feet up and down the trunk and principal branches, while advancing only a few inches in a radial direction. The hyphae penetrate into all the wood cells. The decaying wood is lighter in color than the sound wood. In the final stages of the decay the wood cracks into cuboidal blocks, with the intervening crevices filled with strands of the white mycelium of the fungus. The decayed wood is somewhat richer in carbon and poorer in oxygen and nitrogen than sound wood.—H. HASSELBRING.

Apogamy in Dasylirion.—WENT and BLAAUW[22] have described apogamy in *Dasylirion acrotrichum*, in the case of plants in cultivation in the Utrecht Botanical Garden. This Mexican species is dioecious, and no staminate plants exist in the garden, thus precluding the possibility of fertilization. A certain number of fruits matured sufficiently to attract attention, and an examination of the ovules discovered embryo sacs containing endosperm tissue in various stages of development, in some cases completely filling the sac. Dasylirion is thus added to the very few illustrations of endosperm-formation without fertilization. In these endosperm-containing sacs no embryos were found, but in some others a group of cells was discovered in the usual position of the egg-apparatus, which the authors seem justified, judging from the figures, in regarding as a young embryo. The position would suggest a case of parthenogenesis, but there is room for doubt, and the authors prefer to speak of it as a case of apogamy.—J. M. C.

[21] BULLER, A. H. REGINALD, The biology of *Polyporus squamosus* Huds., a timber-destroying fungus. Jour. Econ. Biol. 1:101–138. *pls.* 5–9. 1906.

[22] WENT, F. E. F. C. and BLAAUW, A. H., A case of apogamy with *Dasylirion acrotrichum* Zucc. Recueil Trav. Bot. Néerland. no. 3. pp. 12. *pls.* 5. 1905.

Photosynthesis by carotin.—KOHL[23] shows by new experiments that the secondary maximum in the curve of photosynthesis, as drawn by ENGELMANN, is due to carotin. He eliminates the possible error in this determination (made by an improvement of the bacterial method), showing that the bacteria are in no-wise affected by the F-rays alone. But when algae are illuminated only by rays absorbed by carotin, the movement of the bacteria begins, indicating evolution of O_2. He also shows that though O_2 is necessary to the formation of chlorophyll, etiolated leaves may become green in an O-free chamber, provided CO_2 is not in excess, since they can use the O_2 set free in photosynthesis. Of etiolin KOHL can find no trace, and he holds it certain that neither carotin nor xanthophyll (the latter probably a transformation product of the former) can be antecedents of chlorophyll. Whatever gives rise to it is probably colorless.—C. R. B.

Poisonous Colorado plants.—GLOVER[24] reports the results of studies of larkspur and other poisonous plants in Colorado. Of the eighteen species of Delphinium found in Colorado the most serious pests in this connection are *D. elongatum* and *D. Nelsonii*. He finds that the larkspur gradually becomes less and less toxic as it approaches the flowering period and finally becomes entirely harmless. The toxic principle has not yet been determined for these species, but is probably delphinine and some other related alkaloids. Other poisonous plants mentioned are species of Zygadenus, Cicuta, Lupinus, and Hymenoxys. The last plant is not strictly poisonous, but forms after being eaten a rubbery mass that may prove injurious. The bulletin contains a useful bibliography of the literature of plants poisonous to cattle on the range.—E. MEAD WILCOX.

Ecology in the Philippines.—It is a matter of no small interest to receive the first extended ecological study of a region of the Philippines. WHITFORD'S[25] account of the vegetation of the Lamao forest reserve introduces us to a tropical region, where the details of plant ecology are new and fascinating, and where the problems must be peculiarly complex. The Lamao forest reserve is in the province of Bataan (Luzon), on the east slope of a group of volcanic peaks known as Mount Mariveles. After the introductory statements as to geology and physiography, climate, and soil, the vegetation is discussed at length under six formations: Strand, Bambusa-Parkia, Anisoptera-Strombosia, Dipterocarpus-Shorea, Shorea-Plectronia, and Eugenia-Vaccinium. The half-tone plates are numerous and present most interesting views of tropical vegetation.—J. M. C.

---

[23] KOHL, F. G., Die assimilatorische Funktion des Karotins. Ber. Deutsch. Bot. Gesells. **24**:222–229. 1906.

[24] GLOVER, G. H., Larkspur and other poisonous plants. Bull. Col. Exp. Sta. **113**:1–24. *pls. 1–8*. 1906.

[25] WHITFORD, H. N., The vegetation of the Lamao forest reserve. Philippine Jour. Sci. **1**:373–431, 637–679. *map* and *pls. 1–45*. 1906.

Azotobacter.—STOKLASA and his assistants have been cultivating *Azotobacter chroococcum* and *Radiobacter* sp. to determine the fixation of nitrogen and the fermentative respiratory activity.[26] They do not confirm BEIJERINCK'S assertion that Radiobacter fixes free N, nor that Azotobacter in company therewith fixes more N than in pure culture. They conceive the fermentation of the mannits and of glucose by Azotobacter to be wrought by glycolytic enzymes which split them into lactic, acetic, and formic acids and alcohol. By the decomposition of these, CO_2 and H_2 are produced, the former at greater rate than in any organisms previously known. Thus 1^{gm} of Azotobacter, dry weight, produces on an average 1.3^{gm} CO_2 in 24 hours. The H_2 is believed to have an important rôle in the fixation of N.—C. R. B.

Subalpine scrub in New Zealand.—COCKAYNE[27] has named the distinct zone of plants on many New Zealand mountains between the limit of the forest and the subalpine meadow the "subalpine scrub." On Mount Fyffe this formation differs from the typical one in the paucity of species and in the great domination of *Cassinia albida*, a species peculiar to that locality, in places being almost a pure formation. *Ranunculus lobulatus*, another local species, is the principal plant beneath the scrub. Some of the shrubs are strongly xerophytic; and the author thinks that the amount of xerophylly observed in many New Zealand plants is by no means a measure of their adaptation to present environment, but rather a survival from previous more xerophytic conditions.—J. M. C.

Monoecism of Funaria hygrometrica.—BOODLE[28] has undertaken to settle the contradictory statements in reference to the distribution of the male and female organs of this species. It seems that bryological works describe it as monoecious; and that certain general textbooks speak of it as dioecious. It turns out that the bryologists are right, as might have been expected. "The male axis bears a terminal male flower, and produces a lateral branch (innovation) which forms a terminal female flower. The female branch may be inserted at different levels, sometimes high up, sometimes basally; it usually has a tuberous base bearing a tuft of rhizoids, and if torn away appears like an independent plant."—J. M. C.

Color of algae.—GAIDUKOV exposed the blue-green plates of Phormidium and the red Porphyra to the spectrum of a strong electric light.[29] In ten hours under all the green to violet rays the color had become yellow to brown-yellow,

[26] STOKLASA, J., et al., Ueber die chemischen Vorgänge bei der Assimilation des elementaren Stickstoffes durch Azotobacter und Radiobacter. Ber. Deutsch. Bot. Gesells. **24**:22–32. 1906.

[27] COCKAYNE, L., Notes on the subalpine scrub of Mount Fyffe. Trans. N. Z. Inst. **38**: 361–374. 1906.

[28] BOODLE, L. A., The monoecism of *Funaria hygrometrica* Sibth. Annals of Botany **20**:293–299. 1906.

[29] GAIDUKOV, N., Die komplementäre chromatische Adaptation bei Porphyra und Phormidium. Ber. Deutsch. Bot. Gesells. **24**:1–5. 1906.

remaining blue-green under the red to yellow rays. Porphyra remained red in the green-violet, but became green in the red-yellow. The pigments thus become of the complementary color to the incident light, and change in a time inversely proportional to the intensity of the light. The same change, but much slower, had been observed by the author in nature, and he considers this complementary chromatic adaptation the chief factor in determining the color of algae.—C. R. B.

Pollen tubes of Cucurbitaceae.—KIRKWOOD[30] has been studying the behavior of the pollen tubes of *Melothria pendula*, *Micrampelis lobata*, and *Cyclanthera explodens*. He has noted that the time elapsing between pollination and the arrival of the tube at the embryo sac in these species is 26, 19, and 41 hours respectively. The tubes pass chiefly over the surface of the conducting tissue, lining the stylar canal and covering the "placental lobes," and this is rich in starch. The suggestion is made that the tube is directed by "nutritive substances secreted by the conducting tissue," and that it "comes under the influence of a stronger stimulant emanating from the ovule," and "the source of this stimulus may be the endosperm nucleus."—J. M. C.

Morphology of Phyllocladus.—Miss ROBERTSON[31] has obtained some glimpses of Podocarpus from cultivated species and five collections of *P. alpinus* secured in New Zealand by Dr. COCKAYNE during 1902, 1903, and 1904. It is disappointing to learn that no critical stages were fixed, and that we are still on the outside of this interesting genus. However, it is of no small interest to learn that centripetal xylem occurs in the cladodes and is restricted to them. This feature is quite characteristic of the Taxus-forms; while the winged pollen grains belong to the Podocarpus-forms. These and other characters emphasize the intermediate position of Phyllocladus between the two prominent tribes of Taxaceae.—J. M. C.

Parichnos in recent plants.—HILL[32] has reached the conclusion that parichnos, a name given by BERTRAND to the strand of thin-walled parenchymatous tissue accompanying the leaf trace in a species of Lepidodendron, is represented among living species of Lycopodium and Isoetes by certain mucilage canals. The tissue to which the name was given is simply an early developmental stage of the canal. In recent plants parichnos is restricted chiefly to the sporophylls, as, for example, in *Isoetes Hystrix*, where two canals run longitudinally on each side of the sporangium, but do not extend into the cortex of the stem, as is the case in fossil forms.—J. M. C.

---

[30] KIRKWOOD, JOSEPH EDWARD, The pollen tube in some of the Cucurbitaceae. Bull. Torr. Bot. Club **33**:327–342. *pls. 16–17.* 1906.

[31] ROBERTSON, AGNES, Some points in the morphology of *Phyllocladus alpinus* Hook. Annals of Botany **20**:259–265. *pls. 17–18.* 1906.

[32] HILL, T. G., On the presence of a parichnos in recent plants. Annals of Botany **20**:267–273. *pls. 19–20.* 1906.

Spore formation in Botrychium.—The development of the spores and the behavior of the tapetum in *Botrychium virginianum* are described by STEVENS.[33] CARDIFF had already published an essentially identical account of the tapetum.[34] STEVENS'S term *tapetal plasmodium* seems to be a suggestive and convenient name for the peculiar tapetal mass as it appears in Botrychium and many other pteridophytes. The behavior of the kinoplasm and trophoplasm during the formation of spores from the mother cell indicates that these two plasms are interchangeable, each being able to become transformed into the other.—CHARLES J. CHAMBERLAIN.

Dichotomous leaves in Cycas.—SEWARD[35] has called attention to the dichotomous leaves of *C. Micholitzii*, a subterranean-stemmed species from Annam. Most of the pinnae are repeatedly dichotomous, but the terminal pinnae are simple and similar to those of other species of the genus. It seems that dichotomous pinnae in the cycads were first noted by MOORE in the Australian *Macrozamia heteromera*. The author suggests the possibility that the usual simple pinnate type of the cycadean leaf "may be the result of reduction from an older type characterized by the more primitive dichotomous habit."—J. M. C.

Diatomin.—KOHL was incited by the papers of MOLISCH[36] and TSWETT[37] to reinvestigate the coloring matter of diatoms,[38] having denied in his work on carotin the existence of a special pigment, "diatomin." He now finds that his conclusion was correct as regards any special "diatomin; " but the pigment is not carotin and xanthophyll alone, as he declared, chlorophyll, with the same absorption spectrum as in higher plants, being also present. The leucocyan of MOLISCH he does not find. The yellowish or brownish hue of the diatoms is due to the prevalence of carotin as compared with the higher plants.—C. R. B.

Germination in Ophioglossum.—The difficulty and the desirability of securing the germination of the spores of the pteriodophytes with tuberous gametophytes are well known. CAMPBELL announces (Annals Bot. **20**: 321) in a brief note that he has secured germination in certain Javanese species of Ophioglossum. In every case the characteristic endophytic fungus was present beyond the three-celled stage. In one case a gametophyte of thirteen cells was found; but no stage between this and mature gametophytes were secured.—J. M. C.

---

[33] STEVENS, W. C., Spore formation in *Botrychium virginianum*. Annals of Bot. **19**:465–474. *pls. 18–20*. 1906.

[34] CARDIFF, I. D., The development of the sporangium of Botrychium. BOT. GAZETTE **39**:340–347. *pl. 9*. 1905.

[35] SEWARD, A. C., Notes on Cycads. Proc. Cambridge Phil. Soc. **13**:293–302. 1906.

[36] MOLISCH, H., Bot. Zeit. **63**[1]:131–162. 1905.

[37] TSWETT, M., *ibid.* 273–278.

[38] KOHL, F. G., Die Farbstoffe der Diatomeen-Chromatophoren. Ber. Deutsch. Bot. Gesells. **24**:124–134. 1906.

Cytology of Entomophthoraceae.—One species of Empusa and four of Entomophthora have been studied by Riddle.[39] In Entomophthora the division is more or less typically mitotic. During prophase the chromosomes are formed by a direct aggregation of the chromatin granules without the previous formation of a spirem. In the formation of zygospores the fusing bodies are coenogametes. The writer suggests that the azygospore of Empusa is of the nature of a chlamydospore. Cytological conditions indicate that Entomophthora is a more highly developed genus than Empusa.—CHARLES J. CHAMBERLAIN.

Lime and sphagna.—As a result of cultures PAUL, in a preliminary paper,[40] confirms the older and still prevalent idea that the sphagna are very sensitive to the presence of $CaCO_3$ in the water in which they grow, and controverts the pronouncements of WEBER and of GRAEBNER. *Sphagnum rubellum* is most sensitive, bearing less than 77^{mg} $CaCO_3$ per liter (i. e., 0.0077%), while *S. recurvum*, least sensitive, bears less than 312^{mg}. *S. rubellum* changes its beautiful red to a blue, indicating an alkaline reaction, the more clearly the higher the lime content of the solution.—C. R. B.

Julianiaceae.—Under this name HEMSLEY[41] has established a new family of Mexican plants, known at present to contain two genera (Juliania and Orthopterygium) and five species. Its closest relationships are said to be with the Anacardiaceae and Cupuliferae; but the final judgment of the author places it in linear arrangement between Juglandaceae and Cupuliferae. "The absolute separation of the sexes and the very great diversity of the floral structure of the sexes, associated with pinnate leaves, offers a combination of characters probably without a parallel."—J. M. C.

Fossombronia.—HUMPHREY has described[42] in detail the germination of the spores and the development of the sex organs of a Californian species, *F. longiseta*, the first investigation of any member of the genus since LEITGEB's, nearly 30 years ago. No striking anomalies appear. No centrosome was observed at any stage of nuclear division; blepharoplasts seem to appear *de novo*, and a *Nebenkörper* likewise, forming the middle piece of the sperm. The spermatids are of the pyramidal form described by IKENO in Marchantia, with no wall between the pair.—C. R. B.

---

[39] RIDDLE, LINCOLN W., Contributions to the cytology of the Entomophthoraceae; preliminary communication. Rhodora **8**:67–68. 1906.

[40] PAUL, H., Zur Kalkfeindlichkeitsfrage der Torfmoose. Ber. Deutsch. Bot. Gesells. **24**:148–154. 1906.

[41] HEMSLEY, W. BOTTING, On the Julianiaceae, a new natural order of plants. Abstract. Read before Royal Society, London, June 28, 1906.

[42] HUMPHREY, H. B., The development of *Fossombronia longiseta* Aust. Annals of Botany **20**:83–108. *pls. 5–6.* 1906.

Anatomy of the Araliaceae.—VAN TIEGHEM[43] has published the results of a very extended anatomical study of the Araliaceae as a basis for their classification. He is convinced that he has discovered anatomical characters that are of great service in this way, and he applies them in establishing groups of genera, in making diagnoses of genera more precise, and in clearing up the positions of a number of critical species. The following six new genera are characterized: *Bonnierella, Mesopanax, Plerandropsis, Octotheca, Strobilopanax, Schizomeryta.* —J. M. C.

Germination among palms.—GATIN[44] has published an extended study of germination among palms, having included in his researches 58 species, representing 33 genera. The first and far the larger part of the paper deals with what are called "anatomical" studies, and one conclusion that is reached, among several others, is that the "cotyledon," so far as palms are concerned, is a single leaf and not a phylogenetic coalescence of two leaves. The second part deals with the chemistry of germination.—J. M. C.

Water relations of the coconut.—The anatomy of the root and leaf of this palm, as well as the conditions affecting the entrance and passage of water through the plant, have been investigated by COPELAND.[45] Maximum transpiration is found to favor maximum yield of fruit. Wind and intense sunlight accelerate transpiration. The roots should be abundantly supplied with water, though an excess is injurious. Irrigation is altogether practical.—RAYMOND H. POND.

Fossil roots of Sequoia.—LIGNIER[46] has identified the roots called *Radiculites reticulatus* as those of Sequoia, or of some allied form as Taxodium. The material studied is from the Stephanian of Grand' Croix, and its distinguishing feature is the reticulated cortical parenchyma. Comparing it with roots of similar structure in living plants, the conclusion is reached that it most nearly resembles the structure observed in the root of *Sequoia gigantea.*—J. M. C.

N. Am. Vernonieae.—GLEASON[47] has published a revision of the North American species of Vernonieae. Seventeen genera are characterized, two of which (*Eremosis* and *Orthopappus*) are new. The species number 143, of which 28 are new. The large genus is Vernonia, with 99 species, 25 of which are new; and the new genus Eremosis includes 15 species, 13 of which have heretofore been assigned usually to Vernonia.—J. M. C.

---

[43] VAN TIEGHEM, PH., Recherches anatomiques sur la classification des Araliacées. Ann. Sci. Nat. Bot. IX. **4**:1–208. *figs. 54.* 1906.

[44] GATIN, C., Recherches sur la germination des palmiers. Ann. Sci. Nat. Bot. IX. **3**:191–315. *pls. 11. figs. 58.* 1906.

[45] COPELAND, E. B., On the water relations of the coconut palm. Philippine Jour. Sci. **1**: 6–57. *pls. 3.* 1906.

[46] LIGNIER, O., *Radiculites reticulatus*, radicelle fossile de Séquoinée. Bull. Soc. Bot. France IV. **6**:193–201. *figs. 5.* 1906.

[47] GLEASON, H. A., A revision of the North American Vernonieae. Bull. N. Y. Bot. Gard. **4**:144–243. 1906.

Apical meristems of monocotyl roots.—DAISY G. SCOTT[48] has investigated the root tips of Alisma, Butomus, Vallisneria, Ruppia, Zostera, Naias, Stratiotes, and Limnocharis. Her results support DE BARY'S statement in reference to the roots of monocotyledons in general, namely that there are three distinct groups of initials, one giving rise to calyptrogen, another to dermatogen and periblem, and the third to plerome.—J. M. C.

Megaspores of Lepidostrobus.—Mrs. D. H. SCOTT[49] has found that certain megaspores referred to KIDSTON'S Triletes belong to *Lepidostrobus foliaceus*, heretofore regarded as homosporous. They are peculiar in bearing a conspicuous appendage, said to be suggestive of the so-called "swimming apparatus" of Azolla. Many of these spores were found, and they are spoken of as "fairly common objects."—J. M. C.

N. Am. Hydnaceae.—BANKER[50] has published a revision of the pileate forms of Hydnaceae found in North America north of Panama, and including the adjacent islands. A few resupinate forms are included, but in general they are excluded, awaiting an examination of the Berkeley types. Ten genera are presented, two of them being new (*Leaia* and *Grandinioides*), and of the 63 species 10 are new.—J. M. C.

Fossil germinating spores.—SCOTT[51] has announced the discovery of germinating spores in a sporangium of *Stauropteris Oldhamia*. The discovery is important, for it has been in doubt whether this species should be regarded as a fern or a pteridosperm. The germination is distinctly fern-like, and confirms the anatomical resemblance of this species to the Botryopterideae.—J. M. C.

Apple scab.—LAWRENCE[52] reports further studies of the apple scab in Washington. In a comparative test of the relative effects of the dust spray mixture and the ordinary liquid Bordeaux it was found that the liquid was twelve times as effective as the dust spray. This is in accord with the results secured by CRANDALL[53] in Illinois.—E. MEAD WILCOX.

---

[48] SCOTT, DAISY G., The apical meristems of the roots of certain aquatic monocotyledons. New Phytol. **5**:119–129. *pl. 9.* 1906.

[49] SCOTT, RINA, On the megaspore of *Lepidostrobus foliaceus*. New Phytol. **5**:116–19. *pl. 8. figs. 24–25.* 1906.

[50] BANKER, H. J., A contribution to a revision of the North American Hydnaceae. Mem. Torr. Bot. Club **12**: 99–194. 1906.

[51] SCOTT, D. H., The occurrence of germinating spores in *Stauropteris Oldhamia*. New Phytol. **5**:170–172. 1906.

[52] LAWRENCE, W. H., Apple scab in Eastern Washington. Bull. Wash. Exp. Sta. **75**:1–14. 1906.

[53] CRANDALL, C. S., Spraying apples. Relative merits of liquid and dust applications. Bull. Ill. Exp. Sta. **106**:205–242. *pls. 1–9. figs. 1–5.* 1906. Review in BOT. GAZETTE **42**:157. 1906.

NEWS.

DR. H. A. GLEASON has been appointed instructor in botany in the University of Illinois.

F. S. EARLE has retired from the directorship of the Estación Agronómica Central de Cuba.

DR. A. A. LAWSON, Stanford University, has been advanced to an assistant professorship in botany.

C. B. CLARKE, the well-known English systematist, died at Kew August 25, at the age of seventy-four years.

DR. J. N. ROSE, United States National Museum, left August 1 for his sixth collecting trip in Mexico, being especially interested in the Cacti.

PROFESSOR CHARLES FLAHAUT, Montpellier, has been elected an honorary member of the Zoological and Botanical Society of Vienna.—SCIENCE.

MR. JOHN G. HALL, Harvard University, has been appointed assistant in plant pathology in the North Carolina Agricultural Experiment Station.

DURING 1904 the additions to the Kew Herbarium were as follows: 8000 sheets presented by ninety persons and institutions; 4000 sheets purchased.

PROFESSOR C. R. BARNES, Dr. C. J. CHAMBERLAIN, and Dr. W. J. G. LAND, University of Chicago, have spent the month of September in botanical work in Mexico.

DR. H. C. COWLES, University of Chicago, will spend the autumn and early winter in Florida, studying the everglades under a grant from the Carnegie Institution.

DR. A. F. BLAKESLEE has been appointed instructor in cryptogamic botany in Harvard University for the ensuing year, and will also give instruction in Radcliffe College. He has recently returned from two years study at Naples and Halle.

IN COMMEMORATION of the twenty-fifth anniversary of its foundation, September 1907, the German Botanical Society proposes to publish a *Festschrift* of about 300 pages and 20 plates; and distinguished specialists, whether members or not, are asked to offer MSS. before January 1, 1907, to the Secretary, Professor Dr. C. MÜLLER.

THE DEATH OF H. MARSHALL WARD, professor of botany at Cambridge University, is announced as having occurred August 26. He succeeded Professor C. C. BABINGTON at Cambridge in 1895, and died at the age of fifty-two years. His work on plant diseases is well known, and the splendid new botanical building, which was the result of his tireless activity, had only been occupied for two years.

THE *Beihefte zum Botanischen Centralblatt*, heretofore published by GEORG THIEME in Leipzig, will be published, beginning with the twentieth volume, by C. HEINRICH of Dresden. It will continue under the same editors, Drs. OSCAR UHLWORM of Berlin and F. G. KOHL of Marburg, and with the same two sections. The indefinite size of the parts enables the editors to promise publication with the utmost promptness.

THE COMMITTEE on "Applied Botany" of the International Association of Botanists met in Paris August 25–27, fourteen members being present. In addition to the customary addresses, it was decided to appoint a botanist to make a tour of the world to investigate and report upon the "resources of applied botany," the report to be made at the general meeting of the Association in 1908. It was estimated that 20,000 francs would be needed for this purpose, and the selection of a suitably trained botanist was left in the hands of a committee. It was decided to raise the money from various governments and public establishments. A committee was also appointed to investigate the invasions of plant diseases and to attempt to secure international legislation in reference to them.

A TIMELY MOVEMENT has been started in New Zealand to preserve the "Riccarton Bush." This fact is of great interest to botanists in general, for this "Bush" is the only remaining portion of a vast forest that once covered the region, and is the last piece of forest of its kind in the world. It is near the city of Christchurch, and a list of its species shows a combination of rare plants that exists in no other place. The dominant tree is *Podocarpus dacrydioides*, and other large trees are *P. totarra*, *P. spicatus*, *Elaeocarpus dentatus*, and *E. Hookerianus*. If this forest were destroyed, it would be a distinct loss to botanical science, which for years to come will need the material it can supply. The government of New Zealand has voted £1500 toward its acquisition, and there is still some £5000 to raise. It is to be hoped that nothing will interfere with the success of this movement. Those interested in it may communicate with Dr. L. COCKAYNE, Ollivier's Road, Christchurch, N. Z.